THESIS

UNPACKING THE TRUNK: PELVIC-THORACIC RELATIONSHIPS IN MODERN *HOMO SAPIENS*

Submitted by

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ABSTRACT

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It is generally accepted that throughout the history of the genus *Homo*, shifts in body morphology have aligned with the emergence of distinct hominin populations (Ruff, 1991, 1994, 2010; Schmid et al., 2013; Walker & Leakey, 1993). The human trunk, comprised of the ribcage, pelvis, and spine, contributes the most to overall body shape. However, how the thorax and pelvis are morphologically related in modern humans is not well understood. The fragmented nature of the human fossil record poses challenges in reconstructing the morphology of the trunk. Research on extant nonhuman ape morphology has suggested covariance between the inferior ribcage and upper pelvis, and it has been proposed that this pattern holds for premodern hominin groups (Schmid, 1983; Schmid et al., 2013).

This expectation of covariance between the upper and lower portions of the trunk has allowed researchers to infer body shape and size with incomplete remains (Schmid, 1983; Schmid et al., 2013; Jellema et al., 1993). However, recent findings have served to challenge previously accepted trends in hominin body shape, calling into question whether the hominin trunk is integrated as was previously thought (Arsuaga et al., 1999; Day, 1971; Rosenberg, 2007; Simpson et al., 2008). The current study expands on previous work by Torres-Tamayo et al. (2018, 2020). Five linear measurements from a mixed sample of 85 living humans were taken from computed topography scans rendered in 3D. Results suggest a minimal correlation between pelvic dimensions and inferior ribcage width, with some variations observed by sex. Understanding this relationship in modern humans aids in evaluating researchers' expectations when interpreting past hominin body shapes and offers new insights into the origins of modern human and neandertal anatomy. Since evidence of integration is weak, results suggest that the thorax and pelvis may be under different selective pressures in modern *H. sapiens.*

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CHAPTER I

INTRODUCTION

Throughout the evolutionary history of the genus *Homo* many changes to body size and shape have been documented and discussed regarding different hominin groups (Ruff, 1991, 1994, 2010; Schmid et al., 2013; Walker & Leakey, 1993). For example, our own modern human body shape is generally accepted to have first arisen in *Homo erectus,* while the wider-trunk, short-limbed bodies of neandertals have been understood as adaptive in many different contexts (Ocobock et al., 2021; Walker & Leakey, 1993; Wang & Crompton, 2004; Rightmire, 1991; Ruff, 1994). neandertal body shape and limb size have often been described as adaptive for thermoregulation in cold climates, high-protein diets, or as specific to certain types of rigorous physical activity that are behaviorally associated with this human group, like sprinting and quickly navigating steep terrain (Ocobock et al., 2021; Ruff, 1991; Stewart et al., 2019). A modern human-like body shape has been conversely interpreted as adaptive for effective locomotion over long distances, load carrying, thermoregulation in open, warm climates, and successful childbirth of encephalized infants in *H. erectus* (Bramble & Lieberman, 2004; Gruss & Schmitt, 2015; Ruff, 1991, 1994; Wang & Crompton, 2004). Yet, the trunk, which significantly influences overall body shape, comprises distinct functional units. Specifically, the ribcage functions to allow respiration and protect vital organs (Schwend et al., 2022). The human pelvis, in turn, is adapted for both successful bipedal locomotion and childbirth (Fischer et al., 2021; Young et al., 2022). It has long been suggested that in early hominins like Australopiths, these areas of the trunk correspond to each other in width and curvature, akin to observations in extant, non-bipedal hominoids (Schmid, 1983; Schmid et al., 2013; Schultz, 1961).

HYPOTHESES AND RESEARCH GOALS

The goal of the current study is to examine the covariance of five linear measurements of the thorax and pelvis taken from computed tomography (CT) scans of 85 individuals. These measurements capture the breadth and depth of both the pelvis and thorax. Since the pelvis is a complex structure, measurements of breadth were taken at both superior and inferior portions of the pelvis and were supplemented by a depth measurement to best capture its overall shape. Pearson's correlation tests are used to measure the strength and direction of relationships and to quantify the relatedness between measurements of the thorax and pelvis in modern humans. The null hypothesis tested in this work is as follows: H_0: The measured relationship between the collected thoracic and pelvic measurements is not significantly different from zero in males and females, respectively. If no significant relationships are found between thoracic and pelvic dimensions, the null hypothesis will not be rejected, and the alternative hypothesis that there are significant relationships between these dimensions will be accepted. If a significant relation is found between these dimensions, the null hypothesis will be rejected, and these relationships can be further investigated. While an ideal world would allow a sufficient sample of complete, articulated *H. erectus* skeletons to be measured in this manner, the incomplete nature of the fossil record has made this an impossibility at present. Instead, the use of CT data collected on modern, living humans allows this proposed relationship in the upper and lower areas of the trunk to be explored.

Despite these advantages, this study is subject to several limitations. The CT data utilized in this study was not collected for the purposes of skeletal measurement and was instead made available for public use after initial collection. As a result, ensuring individuals are in a standard bodily position or point of respiration prior to measuring is impossible. Many individuals were eliminated from the sample as their body positioning did not allow skeletal elements of interest to be scanned in full and were therefore not able to be measured, limiting sample size. In addition to this, any demographic information for this study's sample was limited to the information provided by the initial data collected. Overall, the 85 individuals used in the sample for this study were disproportionately Caucasian, male, and skewed toward ages 40-79 years old. Future studies could benefit from larger, more diverse sample sizes that encompass greater age ranges.

RELEVANCE OF THIS STUDY

The expectation that the trunk is an integrated unit has additionally influenced the reconstruction of later hominin groups and our own understanding of their body shape. Specifically, the most complete *H. erectus* skeleton available to date (KNM-WT 15000) was reconstructed as modern-like and narrow-bodied based partially on the understanding that the superior and inferior portions of the trunk should covary in width and curvature (Jellema et al., 1993). The discovery of this hominin skeleton was potentially one of the most significant in human evolution and, as such, has led to the development and dispersal of many well-accepted ideas about the timing and adaptive context of hominin body proportions in the fossil record. The suggestion that modern body proportions first arose in *Homo erectus* is largely based on the reconstructed KNM-WT 15000, and its discovery has marked the starting point for this idea becoming "almost axiomatic" within the discipline of Paleoanthropology (Holliday, 2012, p. 330). The acceptance of *H. erectus* as a narrow-bodied hominin then established the modern human-like body type as the baseline that subsequent hominins, like Archaic *H. sapiens* and neandertals, are compared to, with neandertal anatomy as a result traditionally being interpreted in environmental and behavioral contexts specific to this particular hominin group (Bastir et al., 2020; Ocobock et al., 2021). The relative completion of the KNM-WT 15000 skeleton and the assumed trunk integration for this individual have then greatly influenced the understanding of hominin body shape and the evolutionary history of modern human proportions.

Subsequent discoveries of *H. erectus* pelvic remains have, however, served to challenge the classification of *H. erectus* as modern-like in body shape. Instead, pelvic remains like OH-28, KNMER-3228, and BSN49/P27 may suggest a wider body shape than previously expected based on the reconstructed trunk of KNM-WT 15000 (Day, 1971; Rose, 1984; Simpson et al., 2008). However, whether a wider *H. erectus* pelvis implies a broader thorax depends on the presumed width relationship between these two areas. It is notoriously difficult to reconstruct upper trunk dimensions as the fragile bones of the ribcage are held together in life by costal cartilage and articulated with vertebrae that themselves are positioned between cartilaginous discs – neither of which preserve well in the fossil record. The current work seeks to take the initial step in establishing and understanding this relationship in the human fossil record by first testing whether or not it exists in modern humans. The current study benefits from taking measurements from CT (Computed Tomography) scans that have been rendered in 3D to explore the relationships between thorax and pelvic dimensions in a sample of extant modern humans. The extent to which the results indicate a species-specific pattern or one that is time-dependent is beyond the scope of the current work. However, relationships observed in the present study are able to either corroborate or complicate those derived from the fossil record.

Previous research that statistically tests trunk integration in modern humans is scarce and has only been undertaken in the recent past, focusing largely on covariation between the three-dimensional shapes of the thorax and pelvis (Torres-Tamayo et al., 2018, 2020). Results, however, suggest either a complicated or nonexistent integration in the human trunk that may differ by ethnicity and sex and demands further investigation into relationships between the thorax and pelvis in modern humans in order to establish a pattern (Torres-Tamayo et al., 2018, 2020). Given the limited scope of prior research, particularly the few investigations of torso integration in modern humans by Torres-Tamayo et al. (2018, 2020), and considering the relatively recent nature of these studies, it is then evident that there exists a pressing need for further investigation into torso integration in modern humans.

Torso integration was observed in extant nonhuman apes and later hypothesized to drive early hominin morphologies with affinities to these apes (Schmid, 1983; Schmid et al., 2013; Schultz, 1961). Similarly, relationships in modern human trunk morphology can set expectations of body shape in later hominin groups, such as *H. erectus, Homo heidelbergensis, and the neandertals.* Determining whether or not a pattern seen in modern humans reflects an ancestral or derived condition is dependent upon our interpretations of the morphology of past human ancestors. The expectations that precede interpretations of traits in human ancestors then serve to shape our own understandings of observable patterns in extant humans. When presented with increasing evidence that contradicts previously held expectations, it is then necessary to re-evaluate and test the beliefs and hypothesized relationships that frame interpretations of the fossil record.

Establishing whether a relatively narrow pelvis correlates with a narrow thorax in modern humans and recent premodern hominin groups is then increasingly significant as newer fossil finds continue to call into question previously established narratives of evolutionary trends in body size. Instead of the linear, narrow body proportions first reported in *H. erectus* after the discovery of KNM-WT 15000, many researchers now agree that *H. erectus* pelvic remains suggest an overall wider body type for *H. erectus* that is unlike that of modern humans (Arsuaga et al., 1999; Day, 1971; Rosenberg, 2007; Simpson et al., 2008). Whether these wider pelves imply a wider ribcage is dependent upon the existence of a strong, positive relationship between these two structures. Establishing if this pattern is present in modern humans is then the first of many steps to understand how far into the hominin evolutionary past torso integration can be expected.

In light of both the aforementioned pelvic discoveries and newer reconstructions of KNM-WT 15000's ribcage, many researchers instead now agree that *H. erectus* possibly exhibited the ancestral condition of a wide trunk observed in *H. heidelbergensis* and neandertals (Bastir et al., 2020). We now anticipate that all members of the genus *Homo* until the appearance of recent *Homo sapiens* should exhibit this pattern of a wide-body (Arsuaga et al., 1999; Bastir et al., 2020; Simpson et al., 2008; Torres-Tamayo et al., 2020). While *H. erectus* was at the center of understanding when modern human-like body proportions arose, the implications of such an understanding are far-reaching. Insight into the timing of changes to the hominin trunk is crucial to determining if modern *H. sapiens* anatomy reflects an ancestral or derived condition. If a modern-human body plant did arise in *H. sapiens* and not *H. erectus,* a re-evaluation of the adaptive contexts of both modern human and neandertal body shapes is then warranted. As will be discussed in greater detail in the following chapters, much of neandertal anatomy is interpreted as specific to this human group's behavior and inhabited climates, representing an anatomical shift away from the modern body plan established with *H. erectus*. However, if the neandertal body shape is instead a continuation of a wide body shape seen in *H. erectus*, it is then the unique modern human body shape that warrants interpretation.

Throughout this work, several anatomical units will be referred to frequently and should, therefore, be defined prior to in-depth discussion. The trunk is an anatomical unit consisting of the ribcage, spine, and pelvis and dictates the general shape of the postcranial body, excluding the appendages (Bastir et al., 2022). The thorax is also an anatomical structure and comprises the upper portion of the trunk. The thorax can be thought of skeletally as consisting of the ribs, thoracic vertebrae, and sternum. The pelvis, as referred to in this work, includes the os coxa, sacrum, and coccyx as an articulated unit.

RELEVANT DEFINITIONS AND DESCRIPTIONS

In addition to the previously described anatomical areas, there are several concepts that will be frequently referred to throughout the body of this work; these include integration and the torso integration hypothesis. Within the study of evolution, different ideas exist about how traits evolve in organisms and within lineages and whether these traits can be considered integrated or modular. Broadly, above the level of individuals and within lineages, integration can be used to describe the coevolution of traits, whereas modular traits evolve somewhat independently of each other (Zelditch & Goswami, 2021). In an evolutionary context, modularity can be the result of singular genes influencing multiple traits and/or natural selection working against integration (Zelditch & Goswami, 2021). Although quantifying integration and modularity are complicated, and there are degrees to both, evolutionary modularity and integration are often understood in terms of patterns of covariation, which should speak to the strength of integration (Klingenberg, 2014). Integration, then, in this work, refers to the idea that structures that coevolve should physically covary with each other.

SYNOPSES OF CHAPTERS

The second chapter of this work will review relevant literature to provide the necessary background and context for the research question this study addresses. This chapter will first provide an overview of morphology exhibited in the fossil record that is consistent with a wide-bodied ancestral condition for genus *Homo*. Chapter II then reviews the implications and potential advantages of both the wide and narrow body proportions in hominin groups. Chapter III provides a description of the data collection methods and sample used in this study. Additionally, Chapter III delivers a detailed account of the statistical methods used to address the research question this work examines. Chapter IV summarizes the results obtained from the statistical analyses described in Chapter III. Chapter IV then discusses the relevance of these results to the research question and hypotheses evaluated in this work. Chapter V offers a synopsis of the results and discusses their implications. Chapter V then summarizes the study and identifies potential direction for future research on this subject.

CHAPTER II

LITERATURE REVIEW

This chapter first discusses the structure and function of the upper and lower trunk, the thorax, and the pelvis. Next, this chapter will detail factors that influence the morphology of these structures throughout the course of the human lifespan. Generally, the purpose of this discussion is dual: firstly, to understand how recent works may shift the understanding of the traits traditionally thought to be ancestral and derived within the genus *Homo*, secondly to review the potential advantages of the traits of interest in modern *Homo sapiens* and premodern members of genus *Homo* alike to establish the significance of studies on covariation between these structures in modern humans. As previously noted, there exists a traditional view that the narrow, linear body shape evolved in the genus *Homo* and corresponded with an ability to traverse longer distances through open environments (Wang & Crompton, 2004). The wide-bodied morphology of neandertals has, in this context, been interpreted as deviating from the narrow body plan thought to be shared by *H. erectus* and modern humans, with neandertal morphology reflecting derived traits as adaptations to harsh climates (Ocobock et al., 2021). However, as the present discussion summarizes, a growing body of evidence supports an alternative pattern, wherein the genus *Homo* exhibits a pattern of wide trunks, evidenced by mediolaterally and anteroposteriorly expanded thorax coupled with a mediolaterally expanded pelvis with flared ilia.

The Thorax and Pelvis: Form and Function of the Modern Human Trunk

As previously noted, the thorax is an anatomical unit that is part of the trunk and can be thought of (skeletally) as consisting of the ribs, thoracic vertebrae, and sternum. Modern human ribcages are often described as “barrel-shaped,” while nonhuman apes are said to have a more "funnel-shaped" thorax (Walker & Leakey, 1993, p. 296). This conical shape has been suggested to be partially due to morphological relatedness between the inferior ribcage and iliac blades; the reoriented bipedal iliac blades of humans necessitate a narrower inferior thorax to accommodate the bipedal pelvis (Jellema et al., 1993). In living humans, the thorax mainly functions to allow respiration to occur and to protect vital organs (Schwend et al., 2022). The ribs dictate the shape and size of this area, and their motion allows for effective respiration (Schwend et al., 2022). In addition, the rib cage appears to also limit the flexibility of the thoracic spine (Sham et al., 2005). The barrel-shaped modern human thorax is achieved early in human life and continues to develop throughout adulthood, changing from a funnel shape to incorporate more mediolateral width in the upper thorax relative to the lower portion by the age of three, Figure 1 depicts these changes (Bastir et al., 2013). Mediolateral width increase appears to be related to lung growth early in life, while at later stages of life, changes in dimensions of the mid-thorax may relate to changes in organs and the lower spine in males (Bastir et al., 2013).

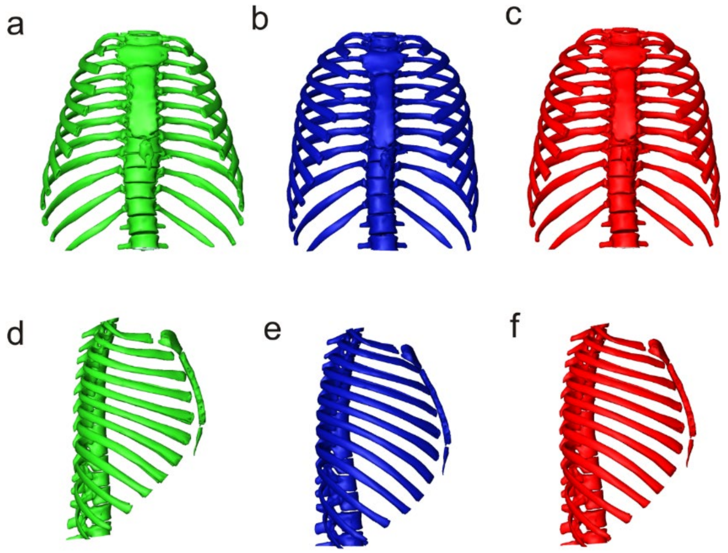

Figure 1: Adapted from Bastir et al. (2013). Comparison of mean ribcage shape in different age groups. Group 1 (green) ages range from newborn to two years of age, Group 2 (blue) ages range from 3-18 years of age, and Group 3 (red) includes individuals over 18 years.

During human evolution, the thorax has undergone many changes, starting with what is often described as a change from a 'funnel' to a 'barrel' shape (Aiello & Wheeler, 1995). The expensive tissue hypothesis states that "metabolically expensive" tissues, such as brain tissue, can expand without changes to basal metabolic rate only at the expense of other tissues; in the case of humans, this suggests that the cost of a large brain is offset by reduction of the gut early in our lineage (Aiello & Wheeler, 1995). This is proposed to have been made possible by changes to the human diet that entail higher quality and easier-to-digest foods (Aiello & Wheeler, 1995). The modern thorax, then, is the result of the cumulative effect of many evolutionary changes over the years and is distinct in shape from that of nonhuman apes and early hominins.

Within modern humans, variations in the size and shape of the thorax appear to follow sexual and eco-geographical patterns. Modern human CT data indicates sexual dimorphism in the thorax that is unrelated to locomotion; generally, it appears that males tend to have wider inferior ribcages than females, among other differences to be discussed in more detail later (Garcia-Martinez et al., 2016). Further studies have suggested differences in climate and adaptations to high altitudes may influence rib shape. Highland Andean populations have been shown to have more voluminous ribcages when compared to lowlanders, while other comparisons of ribs from different modern populations have indicated differences in rib length between climate-adapted populations (Garcia-Martinez et al., 2018; Weinstein, 2017). Specifically, populations that historically inhabit higher latitudes appear to have longer ribs than those closer to the equator, though this is only seen in the inferior ribcage (7-10) (Garcia-Martinez et al., 2018). While the modern human thorax is shaped by a shared evolutionary history, the overall size and shape of this anatomical area appear to vary by sex, geographic area, and age.

The pelvis comprises the lower portion of the trunk, and its form in modern humans is generally shaped by bipedal locomotion and the need to maintain the ability to pass large-brained infants through the birth canal. Like the thorax, the modern human pelvis differs significantly in form from those of nonhuman primates and earlier hominins. Modern humans possess posteriorly oriented, shortened ischia, anteriorly oriented pubic rami, and broad, curved ilia in comparison to nonhuman apes, which are adaptations for bipedalism and are the result of developmental changes that are unique to bipedal hominins (Young et al., 2022). Many of these aspects of the modern human pelvic form are observable in early members of modern *Homo sapiens*, such as Skhul IV, Qafzeh IX, and Omo 1 (Gruss & Shmitt, 2015; Hammond et al., 2017; Marchall, 2000; Rak, 1990).

In modern humans, sexual dimorphism in the pelvis is pronounced; dimensions that are most dimorphic are, unsurprisingly, those that influence the health of the human neonate (Fischer et al., 2021). Although many of the sexually dimorphic aspects of the human pelvis also differ by sex in nonhuman primates, the magnitude of differences is much greater in modern humans and suggests that a more spacious birth canal is strongly selected for in the former out of necessity for the birth of encephalized infants (Fischer et al., 2021). Both the head and shoulders in modern humans must rotate several times to successfully pass through the birth canal, necessitating constraints on pelvic dimensions in females that are not seen in males (Rosenberg & Trevathan, 2002).

Beyond bipedal locomotion and obstetrics, it is well-known that pelvic shape and size in modern humans are also very much influenced by latitude and population history (Betti, 2017;

Ruff 1991, 1994). A cylindrical model of the human body predicts that in colder temperatures, variation in height necessitates a larger breadth in order to maintain an ideal ratio of surface area to mass (Ruff, 1991). Comparisons of Bi-Iliac Breadth and stature in modern humans have corroborated this idea by showing that, despite variation in height, Bi-Iliac Breadth appears to increase as temperatures decrease (Ruff, 1991). In addition to relationships between climate and pelvic breadth, it appears that there may also be differences in birth canal shape that are influenced by latitude (Kurki, 2013). Just as body size differs among populations, dimensions of the birth canal also differ based on body size and, therefore, among populations (Kurki, 2013; Walrath & Glantz, 1996). Specifically, it appears that high-latitude modern humans have greater mediolateral pelvic dimensions overall in addition to having larger birth canals (Kurki, 2013). This is consistent with the well-accepted idea that body surface area relative to mass is increased in warmer climates, while the opposite is true in colder climates (Ruff, 1994). Overall, it is clear and well-accepted that climate, among the other factors previously discussed, influences pelvic morphology in modern humans.

As previously noted, thoracic morphology is influenced by age (among other previously noted factors) in modern humans. This is also true of the modern human pelvis, which undergoes many age-related changes throughout the course of the modern human lifespan. It appears to be the case that these age-related changes themselves differ by sex (Waltenberger et al., 2022). In addition, mechanical factors that bring about bone remodeling result in changes to pelvic shape in postmenopausal women and male modern humans; in premenopausal women, these changes appear to be hormonal (Waltenberger et al., 2022). Specifically, in women, the sacrum initially tilts anteriorly while the pelvic inlet expands mediolaterally until menopause; afterward, changes to pelvic shape are similar between sexes and include reduced iliac height, shortening of the pubis and reduction in pelvic canal dimensions (Waltenberger et al., 2022).

Overall, there are many different factors that influence the morphology of the trunk in modern humans in both sexes. The thoracic and pelvic shapes seen in the genus *Homo* are distinct in many ways from that of nonhuman primates and early hominins. Both the upper and lower portions of the trunk (thorax and pelvis) undergo developmental changes during childhood but also appear to change as a result of age. Many factors influence the dimensions of the pelvis, which is very sexually dimorphic in modern humans, especially when compared to other nonhuman primates. Climate drives differences in pelvic breadth in both sexes, allowing for effective thermoregulation despite variation in height. Pelvic breadth, as a measure of overall body breadth and pelvic inlet size both correspond to differences in temperature between populations. Both the thorax and pelvis perform essential functions for survival and successful evolution, including breathing, locomotion, thermoregulation, and, of course, childbirth.

The Torso Integration Hypothesis: Hominins and Modern Humans

Integration in the trunk has been hypothesized in nonhuman primates and hominins (Schmid, 1983; Schmid et al., 2013; Schultz, 1961). Following this idea, it is expected that shape and width in the lower ribcage should correspond to curvature and width in the iliac blades of the pelvis; this has been proposed to be true in some hominins and influences interpretations of body shape in premodern human groups (Torres-Tamayo et al., 2018). Recent tests of this hypothesis in modern humans, however, imply that integration in the trunk of modern humans is complicated. Some research suggests that covariation between the thorax and pelvis may, in fact, differ by sex and population and suggests that females have narrower thoraces compared to pelves, while the opposite is true in males (Torres-Tamayo et al., 2018). Further research suggests that the broadest portion of the ribcage (mid-thorax) corresponds most with pelvic dimensions in modern humans rather than the inferior thorax, as is suggested for non-human primates (Middleton, 2015). It may be the case that the lower thorax and upper pelvis of modern male *Homo sapiens* are more related to each other than they are in females, though further research using a larger female sample would serve to elucidate these patterns better (Torres-Tamayo et al., 2018, 2020). Although these studies all use data from different populations and answer slightly different research questions, results imply that relationships of curvature and width between the thorax and pelvis may be related to sexual dimorphism.

In light of a potentially sexually dimorphic pattern of torso integration in modern humans, it is important to consider whether or not this pattern is unique to modern humans and how far back it extends into human lineage. Answering this question is the next step to understanding changes in trunk dimensions in the genus *Homo*. Although skeletal remains are necessary to effectively answer the question of whether or not a similar pattern of torso integration is seen in recent hominins (i.e., neandertals), a recent analysis of torso shape covariation in modern humans has been used to take the first step to answer such a question. Specifically, predictive models of thoracic dimensions and shapes based on modern humans have been used to predict the thorax morphology of the Kebara 2 neandertal, which was then compared to previously published thoracic reconstructions (Torres-Tamayo et al., 2020).

The results of this endeavor, however, were complicated and pointed to the need for more studies of torso integration in modern humans that include large sample sizes from diverse populations. It seems to be the case that neandertal thorax morphology can be predicted somewhat accurately based on models of modern human torso integration; however, this result has only been shown to be achievable when using male (or a combined male-female sample) of modern humans and a male neandertal (Torres-Tamayo et al., 2020). In modern females, covariation between the thorax and pelvis was found to be much less pronounced, if present at all; any relatedness identified between the thorax and pelvis was not higher than what can be expected by chance alone (Torres-Tamayo et al., 2020). It should also be noted that it is difficult to truly assess the accuracy of predicted thorax dimensions in the absence of an articulated thorax of a living neandertal. In this case, it did appear that a male sample-based model was a more accurate predictor of neandertal morphology when compared to a physical reconstruction of the Kebara 2, while another Kebara 2 thorax reconstruction (reconstructed as a part of a composite full neandertal skeleton) that included slight differences in thorax width was more consistent with what was predicted from a combined male/female sample of modern humans (Torres-Tamayo et al., 2020). In the absence of an articulated neandertal thorax, any assessments of thoracic and pelvic covariation in neandertals are then limited by the methods and criteria used to reconstruct these portions of the trunk, though better understanding the pattern seen in modern humans is an important step in such assessments. Generally, the few in-vivo studies of torso integration in modern humans that exist have had variable results that appear to be influenced greatly by the proportion of males and females sampled.

New Perspectives on the Human Thorax: Genus *Homo*

As previously noted, the generally accepted view suggests that the genus *Homo* experienced anatomical shifts from a wide to a narrow trunk, with *H. erectus* presenting the first appearance of a modern-like narrower body plan. Initial analyses of KNM-WT 15000 found many affinities with modern humans, including rib shape and thoracic vertebrae, which provided evidence for an anatomical change to more modern-like body shapes in these hominins (Bastir et al., 2020). However, recent reconstruction that accounts for previously unknown vertebral and rib portions has challenged observed thoracic affinities in modern humans. Instead, these findings suggest that the thorax of *Homo erectus* may have more affinities with neandertal morphology than that of modern humans. Quantitative 3D reconstruction has instead revealed KNM-WT 15000 to have greater dimension than that found in modern humans in ribcage shape both mediolaterally and anteroposteriorly, potentially indicating differences in breathing kinematics and a large lung volume (Bastir et al., 2020). Although it is difficult to simulate breathing kinematics in the absence of soft tissue, this reconstruction may suggest that *H. erectus* (in comparison to *H. sapiens*) experienced less superoinferior motion in the thorax with different contribution of the intercostal muscles during inspiration (Bastir et al., 2020). The authors responsible for the reconstruction postulate that this less efficient way of breathing may have been compensated for by overall large volume, which, in turn, is potentially indicative of a larger body mass (Bastir et al., 2020). It should be noted that portions of this skeleton exhibit pathology, though this was accounted for and minimized during reconstruction (Bastir et al., 2020). Although the validity of reconstructions of disarticulated structures can always be questioned, newer methods utilized here suggest the morphology of the *H. erectus* ribcage to be more similar to that of neandertals than modern humans.

The idea that a wide, volumetric thorax is an ancestral trait within the genus *Homo* is not limited to discussions of *Homo erectus*. Rather, the recent reconstruction of the ribcage of KNM-WT 15000 marks an early example of an observable pattern found in subsequent hominins. If this indeed represents the genus *Homo* condition, neandertals no longer deviate from the norm and instead represent it. Reconstruction of one of the most complete neandertal thoraces available appears to support this idea; although the Kebara 2 thorax appears to be like modern humans in terms of size, the shape of the thorax is significantly expanded mediolaterally in the lower portion of the ribcage, as well as anteroposteriorly deeper than proportions seen in modern humans (Gómez-Olivencia et al., 2009). In this case, it would appear that shape rather than size differentiates the upper body anatomy of modern humans and neandertals Gómez-Olivencia et al., 2009).

Old and New Perspectives on Pelvic Morphology

While comparisons of the overall ribcage shape between *Homo erectus,* neandertals, and modern *Homo sapiens* provide an understanding of differences in upper trunk anatomy, the overall body shape of these hominins is also determined by pelvic shape and dimension. If a wide body plan is ancestral to the genus *Homo,* one would expect pelvic dimensions in premodern hominins to correspond to wide thoraces. Recent research has suggested that these structures may covary predictably within modern humans, though more inquiry into this subject is necessary to determine if one can be predicted from the other (Torres-Tamayo et al., 2020). The results of this study will shed light on the strengths of relationships between these structures in modern humans. As previously noted, the pelvis (and thorax) of KNM-WT 15000 was found to have many affinities with the trunks of modern humans upon initial reconstruction. Although this entails a narrow pelvis, if the newly reconstructed ribcage of this individual is to be considered and thoracic dimensions do covary with pelvic ones in *H. erectus, it* should be expected to have a wider pelvis than previously reported. Although the established thoracic dimensions of KNM-WT 15000 have only been recently challenged, broad and flared ilia in fossil human ancestor finds have led past researchers to question the estimated narrow breadth of this specimen's pelvis (Arsuaga et al., 1999). It may be the case that this narrow Bi-Iliac Breadth is a result of the reconstruction process as missing portions of KNM-WT 15000's reconstruction were assessed based on both another incomplete early *Homo* innominate (KNM-ER 3228) and a modern human pelvis, which could skew the reconstructed pelvis toward a narrower, *Homo sapiens*-like breadth (Walker & Leakey, 1993). In addition, the previously mentioned expectation that the ribcage and pelvis should correspond to each other in width and curvature may have also influenced the reconstruction of KNM-WT 15000 as narrow-bodied in comparison to earlier hominins, as this hypothesized relationship was specifically referenced by Jellema et al., (1993) when describing the skeletal reconstruction process. Although the pelvic remains that have been found with associated craniodental material and can be reliably taxonomically identified are not abundant, KNM-WT 15000 does not represent the only fossil hominin with a well-preserved pelvis that has been assigned to *Homo erectus;* further evidence exists to suggest that *H. erectus* may have instead exhibited a wide pelvis when compared to modern humans (Ward et al., 2015).

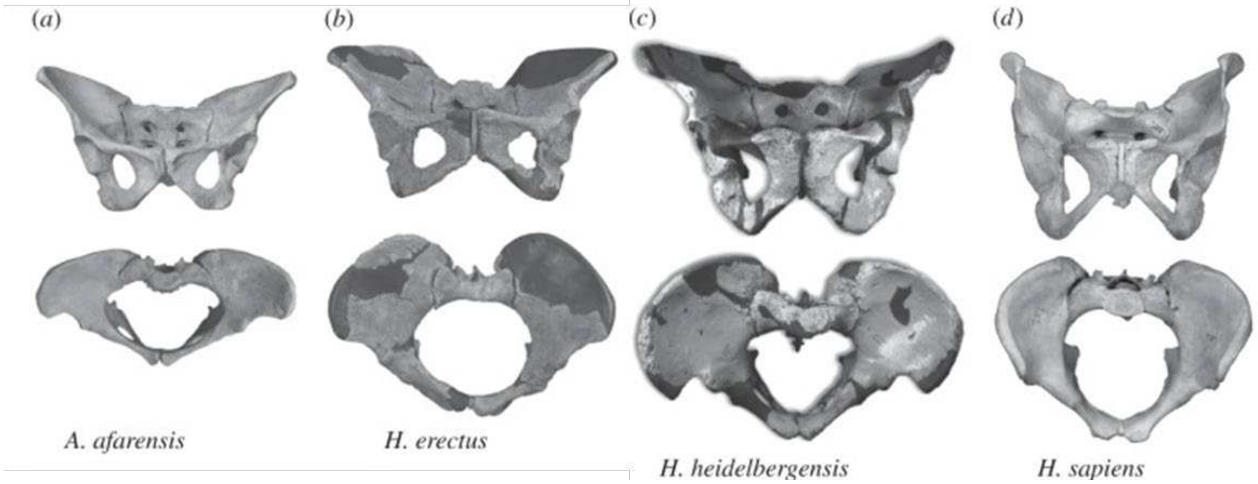

Figure 2: Comparison of pelvic shape between (a) female *A. afarensis* ('Lucy'), (b) female *H. erectus* (Gona), (c) male *H. heidelbergensis* (Atapuerca Pelvis 1), and (d) female modern *H. sapiens;* Adapted from Gruss et al., 2015.

Rather than the narrow pelvic proportions exhibited by the reconstructed KNM-WT 15000, a nearly complete adult female pelvis from Gona, Ethiopia (BSN49/P27) instead shows features of a wide body plan found in later members of the genus *Homo*. Specifically, this individual exhibits Bi-Iliac Breadth outside the average condition of sampled modern humans and is overall broad in the pelvis with flared ilia and a long superior pubic ramus (Simpson et al., 2008). If these finds, alongside the other wide pelves referenced in Figure 2 (instead of the juvenile and pathological KNM-WT 15000), accurately represent the body proportions of *H. erectus*, then a wide body and pelvis are likely found in all premodern members of the genus *Homo*, with modern humans exhibiting derived, narrow proportions (Rosenberg, 2007; Simpson et al., 2008). When the Gona pelvis is considered alongside all premodern pelvic remains that have been assigned to the genus *Homo* it is apparent that KNM-WT 15000 is the only premodern human that exhibits a narrow pelvis (Simpson et al., 2008). It should also be noted that some have questioned the assignment of the Gona specimen to *H. erectus* based on its inferred body size, though the details of this debate are outside the scope of the current discussion (see Ruff, 2010 and Simpson et al., 2014).

Although the Gona pelvis can be considered the most complete pelvis assigned to *H. erectus,* other pelvic remains assigned to this species also fit a wide-bodied morphological pattern. KNMER-3228 is reported to be human-like in overall size but shares morphological affinities with more wide-bodied ancestors (Rose, 1984). Specifically, this specimen has been reported to be like *Australopithecus* in terms of how the ilium forms a “relatively wide angle to the sagittal plane” (Rose, 1984, p. 375). Even less complete but still convincing, the morphology of yet another relatively young specimen assigned to *H. erectus* (OH-28) shares affinities with *H. heidelbergensis* and neandertals; these include flared and laterally biased ilia, which has been argued to suggest that the narrow pelves observed in modern humans are unique to our species (Arsuaga et al.,1999; Day, 1971).

It should be briefly noted that other pelvic remains have been assigned to *H. erectus* but are less complete than previously discussed specimens; UA173/405 has been compared to OH 28 in morphology, but iliac preservation has made effective comparison to modern human populations difficult (Hammond et al., 2018). While 3D surface landmarks of this pelvis have been compared to and found to be within the range of variation in modern humans, it is difficult to assess body shape in this hominin without comparisons of iliac dimensions to modern humans (Hammond et al., 2018). As stated by the original authors: "Due to incomplete preservation of the anterior ilium, it is unclear whether UA 173/405 would have displayed the marked lateral flare of the ilia that results in the wider Bi-Iliac Breadth seen in most Pleistocene *Homo* pelves" (Hammond et al., 2018, p. 122). For these reasons, these pelvic remains have been largely omitted from the discussion of a wide body plan in the fossil record within the current work.

Table 1: *H. erectus* remains discussed, along with associated dates and descriptions.

Fossil	Associated Dates	Region	Wide-Bodied	Sex	Source
BSN49/P27	1.8 - <0.16 Ma	Gona, Ethiopia	Yes	Female	(Simpson et al., 2008)
KNMER-3228	≈1.9 Ma	East Lake Turkana, Kenya	Yes	Male	(Rose, 1984)
OH-28	≈0.5 Ma	Olduvai Gorge, Tanzania	Yes	Female	(Day, 1971; Leakey, 1971)
KNM-WT 15000	1.5 Ma	West Turkana, Kenya	No	Male	(Walker & Leakey, 1993)

Regardless of differing perspectives on taxonomy, a pattern of mediolateral expanded pelves with flaring ilia appears to continue up until the emergence of anatomically modern *Homo sapiens* as all premodern *Homo* pelvic remains with preserved ilia, excluding KNM WT-15000 exhibit wide, flared ilia in comparison to modern humans. These differences in pelvic morphology are observable even in “early anatomically modern fossils pelvises,” which are narrower and present a “low degree of iliac flare” when compared to predecessors (Gruss & Schmitt, 2017, p. 9). Early modern humans like Skhul IV and Omo I exhibit narrow body breadths that are well within the range of modern human variation, and the former can be described as “intermediate between tropical and high latitude modern humans” in pelvic form (Hammond et al., 2017; Ruff et al., 2005, pp. 387-388). While the fragmented state of the Qafzeh IX pelvis makes assessment of the shape of the ilium difficult, the superior pubic ramus is relatively well preserved (Rak, 1990). Though the superior pubic ramus of Qafzeh IX appears long compared to those of warm-climate modern human populations, all measurements of this pelvis fall within the range of modern human variation (Pearson, 2000; Rak, 1990). Perhaps most importantly, Omo I, the oldest of these specimens, also appears to be narrow-bodied, as the preserved portion of the ilium suggests it was "likely within the range of variation of modern human pelves for the orientation of the ilium” rather than “widely flaring” as is characteristic of other Pleistocene *Homo* species (Hammond et al., 2017, p. 211)

The Middle Pleistocene site Sima de los Huesos has yielded pelvic remains that also fit this morphological pattern: a nearly complete male pelvis that exhibits markedly flared ilia and a long superior pubic ramus (Arsuaga et al., 1999). These aspects of this individual’s pelvic morphology have been presented as evidence for wide bodies as a plesiomorphic condition based on the shared morphology between OH-28, neandertals, and other premodern hominins (Arsuaga et al., 1999). It is well known that individuals from this site and other archaic *Homo sapiens* exhibit mediolateral expansion in the pelvis when compared to modern *Homo sapiens* (Gruss & Schmitt, 2015). These observations confirm a pattern of mediolaterally expanded pelves and flared ilia shared between *Australopithecus, H. erectus,* and Archaic *Homo sapiens* and lend support to the idea that it is modern humans, rather than neandertals who deviate from the established morphological pattern.

If it is indeed the case that a mediolaterally-wide body plan defines the genus *Homo* prior to the emergence of modern *Homo sapiens,* then neandertals should be expected to share this morphology. Unlike *H. erectus*, there is little, if any, contention around the idea that neandertals exhibit a wide body plan that is readily observable in the pelvis and thorax. The Kebara 2 individual (whose ribcage was previously described in this discussion) exhibits the morphology expected of a neandertal, which has been used as a baseline for a wide body plan in the present discussion. Kebara 2 and other neandertals all exhibit wide, flaring ilia, mediolaterally broad pelves, and long superior pubic rami (Rosenberg, 2007; Sawyer & Maley, 2005). While this description does not conflict with the accepted understanding of neandertal morphology, the pelvic and thoracic affinities with the fossil specimens discussed in this section warrant a new understanding of this condition; if it is plesiomorphic within the genus *Homo,* a wide trunk's significance should no longer be understood in terms of behavior and anatomy that separates neandertals from the rest of genus *Homo*.

Table 2: Summary of proposed advantages of wide and narrow pelvic breadths

Pelvic Breadth	Wide	Narrow
Thermoregulation Advantages	Less heat dissipation compared to production, adaptative for cold temperature climates (Ruff, 1994)	Greater heat dissipation compared to production, adaptive for warm temperature climates. (Ruff, 1994)
Locomotion Advantages	Efficient walking in the form of longer strides, less cost (measured per stride) for a given distance, and less muscular movement (Gruss et al., 2017) Ideal for short, powerful bursts of motion (Bastir et al., 2022)	Ideal for endurance exercise (Pomeroy, 2023). Reducing knee injury for endurance locomotion (Cowan et al., 1996; Emami et al., 2007)
Birthing Advantages	Ideal for birthing wide-shouldered infants. (DeSilva et al., 2017)	Anteroposteriorly expanded pelves are ideal for birthing large-brained infants, though mediolateral width is maintained in the absence of rotational birth (Gruss & Schmitt, 2015).
Associated Hominins	Australopiths, *H. erectus*, Archaic *H. sapiens,* neandertals	*H. erectus* (KNM-WT 15000), *H. sapiens*

Advantages of a Wide Body Plan: Perspectives on neandertal Morphology

While it is widely accepted that neandertal anatomy reflects an adaptation to harsh, cold climates, reconsideration of the ancestral body plan warrants reconsideration of the potential advantages of a wide body that is not specific to climate. Although the potential benefits of a wide body and short limbs for those inhabiting cold climates have been discussed in detail, the physiological relationship of many of these features to their proposed adaptive functions has not been tested in modern human populations (Ocobock et al., 2021). For example, neandertal wide lower thoraces have been explained as a means of increasing body mass, accommodating an enlarged liver, or attributed to greater lung capacity (Ocobock et al., 2021). Generally, the discussion of neandertal cold adaptation is framed within the context of Bergmann's and Allen's rules, the former of which predicts an inverse relationship between body size and temperature (Ocobock et al., 2021).

While it is well-established in modern humans that greater body breadth (Bi-Iliac Breadth) allows a decrease in the ratio of surface area to body mass (which in turn minimizes heat dissipation as an adaptation to lower temperatures), this relationship is not the only advantage of a wider pelvis (Ruff, 1994). If it is indeed the case that a wide body plan is observable throughout the genus *Homo* and generally conforms to the ecogeographic patterning present today, it should be expected that hominin groups associated with wider body plans occupied colder climates. However, not all wide-bodied individuals or hominin groups in the human fossil record lived in low-temperature environments (see Table 1). Even neandertals, whose unique attributes are often explained solely as cold adaptations, did not exclusively occupy frigid climates (Ocobock et al., 2021). Potential climatic adaptations aside, it appears that a wide body may be advantageous for specific forms of locomotion. Walking kinematics in modern humans have been studied in this context; findings indicate that individuals with wider pelves have a longer stride at any given speed, resulting in more efficient locomotion for shorter-limbed individuals (Gruss et al., 2017). In addition to a longer stride, which allows overall less energetic cost (fewer strides) for a given distance compared to a shorter stride, individuals with wider pelves are also able to walk with less hip flexion and extension, suggesting a smoother, more efficient way of walking (Gruss et al., 2017). Although these results are used to explain the advantages of a wide pelvis for *A. afarensis*, this relationship has been established in modern humans and should hold true for any wide-bodied obligate biped as much as it does for *A. afarensis* (Gruss et al., 2017).

Empirical tests of the relationship between performance and anatomy in modern humans indicate that a mediolaterally expanded trunk provides advantages for certain types of running. Though no relationship between trunk shape and locomotor function is apparent in lower-intensity exercise, it may be the case that high body mass and robust trunk musculature are better suited for powerful locomotion, like sprinting (Bastir et al., 2022). Functional sprinting does require a longer stride length, and as previously noted, a wider pelvis does indeed beget a longer stride (Bastir et al., 2022; Gruss et al., 2017). If a neandertal's wide body and pelvis served to increase stride length, it could be the case that the exaggerated width seen in neandertal bodies represents not only adaptation to climate but rather adaptation to hunting conditions that necessitate powerful sprinting (Stewart et al., 2019). neandertals did not exclusively occupy cold, harsh areas; many, in fact, lived in more temperate conditions (Ocobock et al., 2021; Stewart et al., 2019). Although there is variation in the climatic conditions these humans were exposed to, neandertals are broadly known to be ambush hunters, which would have necessitated short, powerful bursts of locomotion (Stewart et al., 2019). If trunk musculature needed for effective sprinting corresponds skeletally to a wide, voluminous thorax, the neandertal wide trunk could reflect the importance of certain types of locomotion for survival, though further study on modern humans is required to properly link soft and hard tissue structures in this context (Bastir et al., 2022).

When understanding and reviewing the proposed advantages of wider pelves in premodern hominins, it is essential to acknowledge that there are inherent differences between males and females in any hominin population. Experimental research on modern humans suggests these differences result in further advantages for wide pelves in females, particularly when carrying loads, though this could be partially explained by longer stride length associated with wider pelves (Wall-Scheffler & Myers, 2017). While this discussion reviews the advantages that a wider pelvis may confer based on studies of modern humans, the premodern members of the genus *Homo* discussed so far are included because they fall on the extreme end or outside of the range of variation displayed in sampled modern humans. If a wide trunk is plesiomorphic in the genus *Homo* and exaggerated for specific adaptations in neandertals, as the previously reviewed literature suggests, it is necessary to review the potential advantages of the narrow body plan seen in the trunk of modern *Homo sapiens*.

Advantages of a Narrow Body Plan: Perspectives on Modern Body Proportions

If the narrow proportions seen in the modern human trunk (thorax and pelvis) are the derived condition rather than the ancestral one, it is relevant to discuss the adaptive implications of a narrow body plan. The narrow body plan of modern humans includes a shallower thorax (in comparison to a broad, voluminous one) and a mediolaterally narrower pelvis (Torres-Tamayo et al., 2020). As previously noted, stride length, effective sprinting, and the mediolateral dimensions of the pelvis appear to be related to each other. Other types of locomotion, however, may be more behaviorally relevant to modern humans. Effective endurance running over large distances does not necessarily require long strides in the way that sprinting might; as stride length declines when modern runners are fatigued, stride frequency may be more important for this type of locomotion (Bastir et al., 2022). While increased stride length does correspond to increased running speed, the most successful distance runners are those who are able to maintain their stride length rather than increase it over time (Esteve-Lanao et al., 2008).

It has been suggested that the modern narrow body plan exhibits adaptations to endurance running (Pomeroy, 2023). This idea, combined with an understanding of success in modern distance runners, could suggest a decreased emphasis on increasing stride length and decreased importance placed on pelvic width as a result. Specifically, narrow waist, tall stature, thorax shape, and longer limbs have all been cited as adaptations to endurance running within the genus *Homo* (Pomeroy, 2023). In addition to physical observation, there may also be genetic evidence for an inclination toward endurance exercise in modern *Homo sapiens,* many of whom retain a neutral mutation for a high percentage of slow-twitch muscle (Pomeroy, 2023). neandertal genomes conversely display higher frequencies of alleles associated with "power phenotypes" which may serve as evidence for the importance of different forms of locomotion for these two distinct human groups (Pomeroy, 2023, p. 4).

Sports injury could serve to shed some light on possible advantages of a modern, narrow body plan. While the knee itself is not part of the trunk, the pressure exerted on the lateral portion of the knee joint is directly affected by pelvic width (Emami et al., 2007). Modern human data shows relationships between the risk of knee injury and the size of the angle formed between the distal femur and midline of the body at the knee, referred to in the literature as the quadriceps angle (Cowan et al., 1996). Specifically, it appears that those with larger quadriceps angles (wider pelves) are at an elevated risk of injuries from overuse, namely stress fractures (Cowan et al., 1996). This pattern is also seen in modern human runners, with larger quadriceps angles being a determinant of both knee injury and pain; those with smaller quadriceps angles have significantly lessened risks of injury (Emami et al., 2007; Messier et al., 1991). While this does not necessarily explain why the potentially derived condition of a narrow body plan is seen in modern and not premodern humans, there does appear to be evidence that links pelvic width as an advantage or disadvantage with certain types of locomotion more typical of different hominin groups.

Selective Pressures and the Female Pelvis

While trunk and pelvic shape have implications for locomotion, selective pressures act on the modern human female pelvis that are not limited to locomotion. One of the most well-known arguments for the advantages of a narrower body plan that incorporates human birth and locomotor requirements is Washburn’s obstetric dilemma. This is a hypothesized tradeoff between efficient bipedal movement with a smaller pelvis and the need to maintain enough space for a large-brained infant to pass through (Washburn, 1960). While an in-depth review of the literature surrounding hominin birth mechanisms and the obstetric dilemma is outside the scope of the current discussion, it is impossible to discuss the advantages of a wide or narrow pelvis without reviewing the literature on birthing mechanics in human evolution.

It is apparent that certain dimensions of the female pelvis are under stabilizing selective pressure in encephalized hominins, namely the dimensions of the pelvic midplane and the overall anteroposterior dimensions of the pelvis (Haeusler et al., 2021; Walrath & Glantz, 1996). It is possible that another obstetric dilemma exists as a tradeoff between thermoregulatory and obstetric needs as a result of encephalization. Some have argued that the anteroposterior expansion in the pelvis of *H. erectus* acted to increase pelvic capacity to accommodate larger-brained infants while allowing body proportions that are more effective for thermoregulation in warm climates to persist (Gruss & Schmitt, 2015). It has been proposed that the warm climate origin of modern *Homo sapiens* produced constraints on the width of the pelvis that did not apply to hominins occupying more temperate or cooler climates (Gruss & Schmitt, 2015). This perspective assumes that the narrow-bodied proportions of KNM-WT 15000 are correctly interpreted and representative of other *Homo erectus* individuals.

It may be the case that a non-rotational birth mechanism and broad-shouldered (wide-bodied) infant required a mediolaterally wider pelvis like those observed in premodern genus *Homo* members with anteroposterior expansion accommodating encephalized infants (Gruss & Schmitt, 2015). It should be noted, however, that some suggest a rotational birth was already partially evolved in *Australopithecus afarensis*, though the mediolaterally expanded pelvis can still be understood as a necessity for accommodating a broad-shouldered but smaller-brained infant (DeSilva et al., 2017). Overall, then, the relationships between pelvic dimensions, locomotion, thermoregulation, and obstetrics in the human fossil record are complicated, but the literature suggests relationships exist between brain size and anteroposterior pelvic dimensions alongside shoulder breadth and mediolateral pelvic dimensions in modern and premodern female hominins.

CHAPTER SUMMARY

This chapter provided a review of the relevant literature surrounding interpretations of hominin body shape. If the evidence for an ancestral wide body plan in the genus *Homo* presented in this discussion can be accepted (as understandings of fossil morphology are affected by the accuracy of reconstructed skeletal elements), this warrants a reinterpretation of neanderthal trunk morphology as a plesiomorphic condition, with modern humans representing the exception. Instead of a departure from wide-bodied morphology evident in the long and linear body plan of early and late *Homo*, it seems that relatively recent events in human evolution have instead allowed and encouraged mediolateral and anteroposterior dimensions in the trunk to diminish, with an increase in relative anteroposterior dimension of the pelvis (Torres-Tamayo et al., 2020).

This shift in our understanding of *Homo* body proportions suggests a more nuanced understanding of the differences between modern humans and premodern hominins is needed, as well as a greater understanding of how dimensions of the trunk relate to each other. The results of the present study will shed light on the potential relationships between and within the dimensions of the thorax and pelvis in modern humans. These results will serve to guide future research on the advantages of narrowness and width in these structures and the predictability of thoracic dimensions from pelvic ones in modern humans, which will, in turn, allow for a better understanding of anatomical trends and their significance in the human trunk considering shifting perspectives on when and why these trends arose. The following sections will review the research design, methods, and results to answer the question of how thoracic and pelvic dimensions relate to each other in modern humans.

CHAPTER III

MATERIALS AND METHODS

This study uses CT scans of living individuals to address the research question of whether thoracic and pelvic dimensions covary in modern *Homo sapiens.* First, the sample used in this work, the sample selection process, and the exclusion criteria will be described. The methods used to collect data and their reliability will also be discussed. The statistical methods used to address the research question and test the hypotheses described in Chapter One will then be detailed. Finally, the ethical considerations and limitations of this study that relate to the sample will be described.

SAMPLE

Selection and Exclusion Criteria

This research was conducted using data provided by the Medical Imaging and Data Resource Center, which is funded through the National Institute of Health and provides open-access computed tomography (CT) scans of living individuals taken for studies on COVID-19. To build a suitable sample with regard to size, sex distribution, and anatomical coverage, a file manifest was first downloaded from the MIDRC database that included scans of the abdomen and pelvis of individuals with a minimum age of 30 and a maximum age of 85. Age and imaging area restrictions were put in place to ensure all anatomical areas of interest were visible in scans and that all skeletal elements were fully fused. Individuals were excluded from the sample if their body position made consistent measurements impossible or cut off any area of more than one element of interest from view. Any scans that did not capture both the thorax and pelvis of each individual were excluded. Individuals were also excluded if they exhibited pathology that distorted or prevented measurement on more than one skeletal element. The sample used in this study was selected from all individuals listed in the MIDRC database using the random number generator feature in Microsoft Excel. Each imaging series file corresponds to a unique study, series, and patient ID to distinguish individuals, studies, and files from each other. Individual files from the downloaded file manifest were assigned a random number from 1-4000 using this feature. Two thousand unique values were left after removing duplicate numbers; individuals were subsequently measured in ascending order based on their corresponding random number until 84 individuals were reached. This was done to ensure that the order in which individuals were presented in the database did not affect the sample collected (i.e., to prevent bias if the original manifest listed patients in order of age, sex, or study ID). Additionally, since some scans entered in the database were different CT scans of the same individual taken at different times, any files that shared a patient ID number with a previously measured skeleton were not included in the sample.

Sample Composition

An ideal sample would include an equal number of male and female individuals of varying age ranges from diverse populations to maximize variation within the sample. While the data provided by the MIDRC includes numerous imaging series of males and females of various populations, there are many factors that contribute to the composition of the sample used in this work. The previously described exclusion criteria did not allow the use of the full set of imaging series provided by the MIDRC. Since the data provided by the MIDRC were originally collected to obtain information on COVID-19's effects on the body, most imaging series were initially done with the goal of providing a clear view of the lung area. As a result, a majority of the imaging series available did not include both the full thorax and pelvis and/or were taken on individuals outside of the age ranges necessary for this study.

Most individuals both in the initial dataset provided by the MIDRC and the sample collected for this work were males; in this case, females comprise only 33 of the 85 individuals studied. Table 3 summarizes the age and sex distribution within the sample. In addition to sample size constraints and sex biases, most of the individuals that data was collected on were Caucasian, with only eight African Americans and one individual who was reported as 'American Indian' by the MIDRC. While the total age range of the measured sample spans from 30-85 years of age, 39 of those 84 individuals were aged 60-79; ideally, a sample for this work would be equally divided between age ranges included in the study to minimize and allow adequate accountability for any patterns that may be age-related.

Table 3: Age and Sex Distribution of Sample

Age Range	Number of Individuals in Age Range	Males	Females
30-39	9	7	2
40-59	32	20	12
60-79	39	22	17
80-85	4	2	2
Total	84	51	33

SOFTWARE AND MEASUREMENTS

InVesalius 3.1 is an open-source program that allows users to create 3D models of tissue from computed tomography (CT) scans. While there are many similar programs that will allow users to import CT data in order to extract and measure certain elements, InVesalius 3.1 was chosen due to its ease of use, accessibility, and purported accuracy. Many have found InVesalius

3.1 to be among the more accurate compared to other software packages when compared to manual segmentation of tissue and dry bone measurements (Khan & Tordick, 2018; Lo Giudice et al., 2022; Poleti et al., 2015). For these reasons, InVesalius 3.1 was used to take linear measurements from a 3D rendering of a CT imaging series for the present research.

All data was recorded in an Excel spreadsheet and included demographic, equipment, and health information reported by the MIDRC, as well as measurement data that was collected for this study. All DICOM files provided by the MIDRC were imported into InVesalius 3.1. 3D models of the patients' skeletons were then generated using InVesalius 3.1's preset bone threshold. In some cases, the preset threshold was adjusted until all bony surfaces were visible. Each 3D model of the skeleton was then measured using InVesalius 3.1's linear and measurement tools and was recorded in millimeters. For each measurement landmark chosen by the researcher, InVesalius 3.1 automatically calculates the shortest distance (a straight line) between the chosen landmarks. This software allows users to rotate and enlarge the 3D models of skeletons as necessary to ensure the chosen measurement points are viewable. A set of thirteen initial measurements was taken on each skeleton; if only a single measurement was made impossible by imaging area or patient position, the measurement was excluded, and all other measurements were recorded for that individual. This was done to ensure that the maximum amount of data was able to be collected while maintaining consistency in measurements between individuals.

Thirteen measurements were initially collected and were designed to capture anteroposterior and mediolateral dimensions of the pelvis, as well as thoracic breadth and depth. Measurements were later excluded due to missing data and/or redundancy. Table 4 provides definitions and names of each measurement taken, showing excluded measurements in gray.

Thoracic measurements include Maximum Transverse Thoracic Diameter (MTTD), Inferior Transverse Thoracic Diameter (ITTD), and Maximum Anteroposterior Thoracic Diameter (MATD). Measurements taken below the thorax include Clavicle Length (CL), Pubis-Ilium Length (PIL), Bi-Iliac Breadth (BIB), Transverse Inlet Diameter (TID), Bispinous Diameter (BSD), Acetabulo-Symphyseal Length (PAC), Anteroposterior Inlet Diameter (AID), Bi-Acetabular Breadth (BAB) and Femoral Head Diameter (FMHD). While the torso integration hypothesis only proposes covariance between the ilia and inferior ribcage, other measurements of the pelvis were included in this analysis to better understand relatedness between the pelvis and thorax overall, as well as differences between sexes in pelvic and thoracic relatedness. For this reason, the breadth and depth of the pelvic inlet (TID and APD), as well as the Bispinous Diameter (BSD), were included, as these dimensions are expected to be sexually dimorphic. Additionally, Bi-Acetabular Breadth was included to account for pelvic breadth below the ilia. Overall, these measurements were included to provide the most information about relatedness between pelvic and thoracic dimensions in modern *Homo sapiens.*

Table 4: Definitions and abbreviations for all measurements, as well as measurements that were eliminated, are shown in gray boxes.

Measurement	Definition	Abbreviation
Maximum Transverse Thoracic Diameter	Transverse distance between the medial aspect of ribs forming the widest point of the ribcage	MTTD
Maximum Anteroposterior Thoracic Diameter	Distance between the posterior surface of the sternum and the anterior surface of the corresponding vertebral body where the greatest anteroposterior dimension is achieved	MATD
Inferior Transverse Thoracic Diameter	Distance between the most medial points of the sternal rib ends of the tenth ribs	ITTD
Clavicle Length	Distance between the middle of the medial portion of the clavicle and the most lateral edge.	CL
Pubis-Ilium Length	Distance from the most superomedial portion of the pubic symphysis to the most lateral portion of the iliac crest	PI
Bihumeral Breadth	Distance from the most lateral point of both humeral heads	BHB
Bi-Iliac Breadth	Distance between the most lateral points of the iliac crests	BIB
Transverse Inlet Diameter	Greatest mediolateral distance within the pelvic inlet	TID
Bispinous Diameter	Distance between the most medial point of both ischial spines	BSD
Acetabulo-symphyseal Length	Distance from the most superomedial portion of the pubic symphysis to the most superior point of the acetabulum	PAC
Anteroposterior Inlet Diameter	Measured from the superior-medial aspect of the pubic symphysis to the sacral promontory	APD
Bi-Acetabular Breadth	Distance between the most superior points of the rim of the acetabula	BAB
Femoral Head Diameter	Maximum superior-inferior diameter of the femoral head	FMHD

STATISTICAL METHODS

The goal of this research is to address the question of whether dimensions of the thorax and pelvis covary by testing for relationships between selected dimensions of each anatomical area. For clarity, the goal of the statistical approach utilized here was to use the simplest means possible to establish broadly the relationship between pelvic and thoracic dimensions in modern *Homo sapiens*. Prior to any statistical testing, measurements with missing data were eliminated. Before relationships *between* pelvic and thoracic dimensions were addressed, relationships *within* the thorax and pelvis were assessed using Spearman's correlation matrices. Measurements were then further excluded based on statistical redundancy (i.e., if thoracic measurement A appeared to be highly correlated to thoracic measurements B, C, and D, only thoracic measurement A was included in subsequent hypothesis tests, as measurements B, C, and D are potentially capturing the same information as measurement A). This process was repeated for pelvic measurements, resulting in six total measurements that were then included for hypothesis testing to compare relationships *between* the thorax and pelvis. Relationships *between* pelvic and thoracic dimensions were formally assessed only after all but six of the initial measurements were eliminated in this manner. Table 4 shows eliminated measurements in gray boxes, while measurements chosen for hypothesis testing are pictured in white boxes.

Additionally, before hypothesis testing, sexual dimorphism in the sample was assessed. Since males outnumber females in the sample (n= 51 and 33, respectively), a Welch's t-test was used to compare means between male and female groups for each measurement, which is preferable for normally distributed data with groups of unequal size (Kim, 2019). Hypotheses were then tested in males and females separately to account for sexual dimorphism in the thorax and pelvis. To test the hypothesis that the collected thoracic and pelvic measurements show a statistically significant linear relationship, Pearson's product-moment correlations were performed between Inferior Transverse Thoracic Diameter and each of the five pelvic measurements described in Table 4 and Figure 3, as this test allows for linear relationships between normally distributed, continuous variables to be assessed (Schober et al., 2018). Figures 3 and 4 depict the measurements used for hypothesis testing.

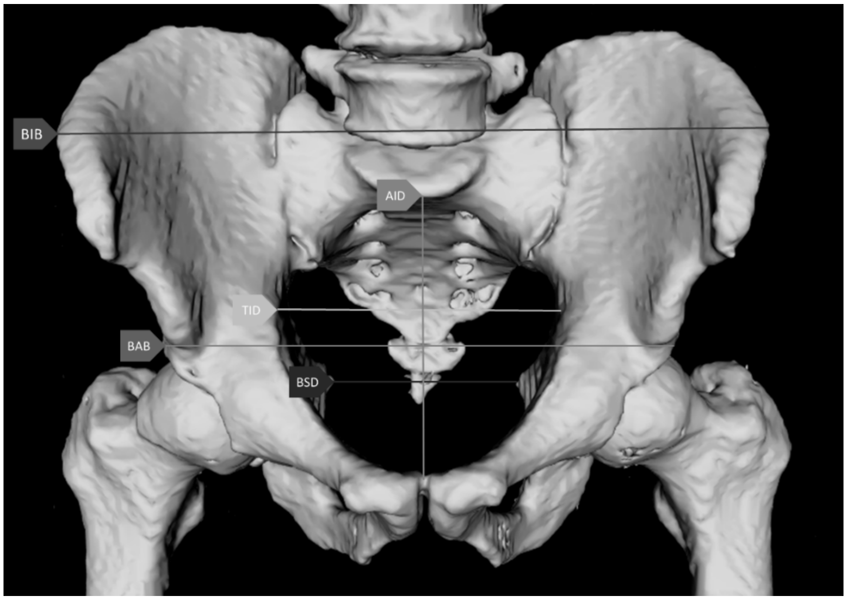

Figure 3: Depiction of pelvic measurements used for hypothesis testing: Bi-Iliac breadth (BIB), Anteroposterior Inlet Diameter (AID), Transverse Inlet Diameter (TID), Bi-Acetabular breadth (BAB), Bispinous Diameter (BSD)

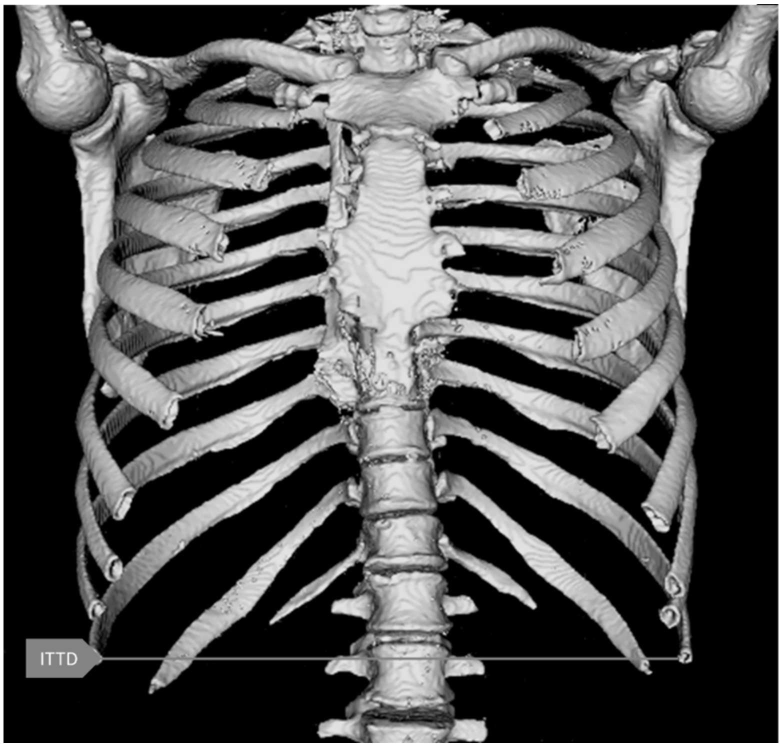

Figure 4: Depiction of Inferior Transverse Thoracic Diameter (ITTD)

CHAPTER SUMMARY

This chapter described the sample selection process, source, and exclusion criteria. This chapter then describes the sample used to address the research question described in Chapter One, providing details about the sample size, selection, and exclusion criteria. This chapter then described the methods used for data collection including software use and measurements chosen. This chapter then described the statistical methods used to evaluate the data and to test the hypothesis described in Chapter One. Finally, this chapter included a brief acknowledgment of the data source and an overview of the ethical considerations taken by the MIDRC when providing data for use in academia and government.

CHAPTER IV

RESULTS

This work tests the null hypothesis that the quantified relationships between collected thoracic and pelvic measurements are not significantly different from zero. The aim of this study is to address the research question of whether the relationships described by the torso integration hypothesis apply to modern *Homo sapiens*. To test this hypothesis, the statistical analyses outlined in Chapter III were conducted. This chapter presents the findings of all statistical analyses undertaken. First, the results of the preliminary Pearson's correlation tests used to eliminate redundant variables will be reported. Next, the results of Welch's t-tests, used to assess the distribution of data and sexual dimorphism within the sample, will be detailed. Subsequently, the hypotheses outlined first in Chapter I will be formally assessed based on the results of Pearson's correlation tests between the five included thoracic and pelvic measurements. Each outcome will be summarized separately for male and female groups.

DESCRIPTIVE STATISTICS & INITIAL ANALYSES

Table 5 provides descriptive statistics for all collected measurements. As noted in Chapter III, prior to any statistical analyses, some measurements were eliminated due to missing data; measurements that were ultimately included for hypothesis testing are listed in Table 8. As described in Chapter III, Prior to testing the hypotheses outlined in Chapter I, some tests were performed on the six included measurements to justify the methods chosen for hypothesis testing. These include Pearson's and Spearman's correlation tests in addition to Welch's t-tests. Correlation matrices (using Pearson's and Sperman's correlations) were generated for thoracic and pelvic measurements to identify and reduce redundant measurements. The Welch's t-tests were then executed to determine if the measures taken were sexually dimorphic and warrant hypothesis testing to be carried out on male (n=51) and female (n=33) samples, respectively. All tests were performed using R Studio version 4.3.1.

Table 5: Descriptive statistics for all measurements

Measurement	Mean	Std Dev	Minimum (mm)	Maximum (mm)
Maximum Anteroposterior Thoracic Diameter	136.47	22.10	85.50	199.50
Maximum Transverse Thoracic Diameter	287.81	27.61	193.80	350.30
Inferior Transverse Thoracic Diameter	277.80	31.86	199.20	350.70
Clavicle Length	148.47	12.84	123.20	178.60
Bihumeral Breadth	334.87	27.38	242.30	388.20
Pubis-Ilium Length	184.80	12.40	126.00	211.10
Bi-Iliac Breadth	275.77	19.41	200.00	324.40
Transverse Inlet Diameter	125.04	9.24	102.90	146.20
Bispinous Diameter	98.42	11.61	68.40	127.40
Acetabulo-Symphyseal Length	118.01	10.76	103.90	199.80
Femoral Head Diameter	46.52	3.53	37.50	53.00
Anteroposterior Inlet Diameter	114.90	10.39	89.60	137.40
Bi-Acetabular Breadth	207.70	10.85	182.70	247.30

Distribution of Data

Prior to any statistical testing, the distribution of data was assessed to ensure that the assumptions of statistical tests were met. Figures 5, 6, and 7 show scatterplots and histograms of all measurements, excluding those that were eliminated due to missing data in males, females, and a combined sample. Acetabulo-symphyseal length and Pubis-Ilium length appeared to be skewed in the combined sample, while all other measurements appeared to follow a normal distribution.

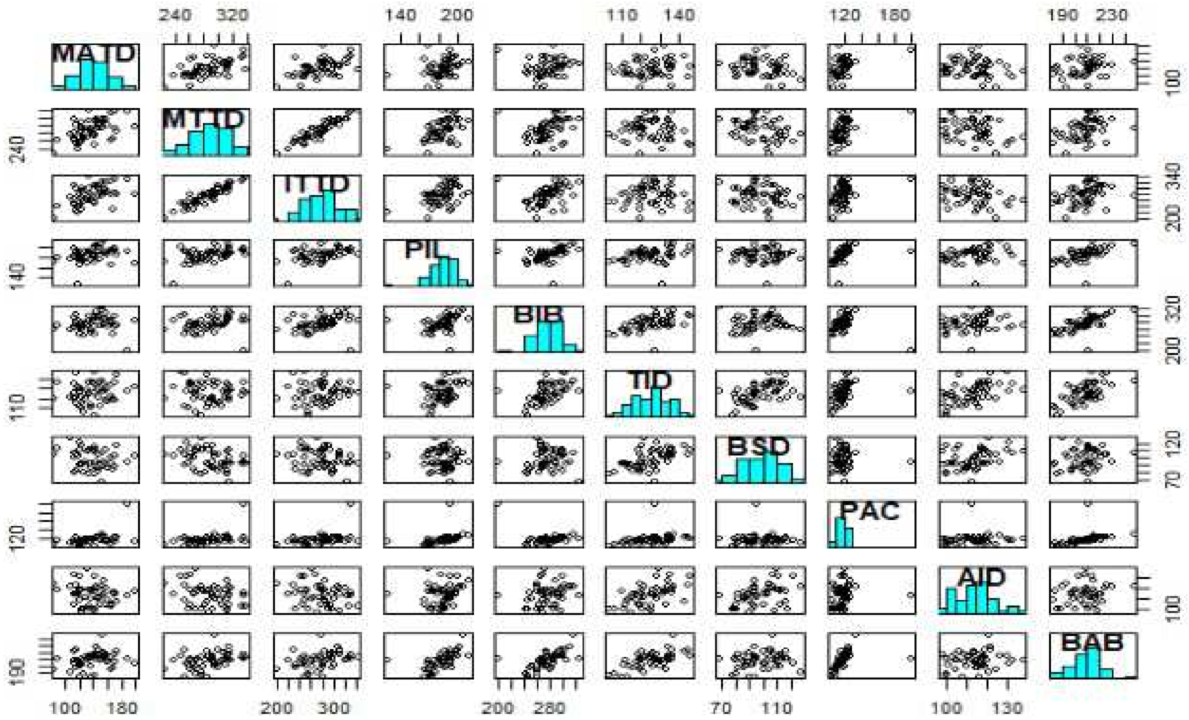

Figure 5: Scatterplots and histograms of measurements, combined sample.

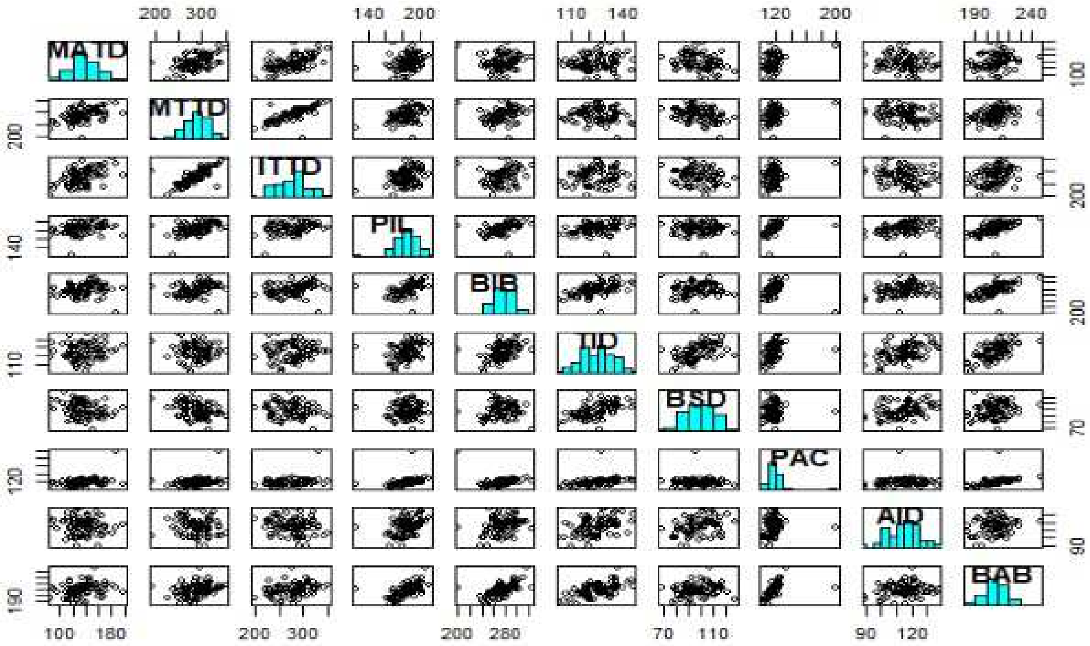

Figure 6: Scatterplots and histograms of measurements, male sample.

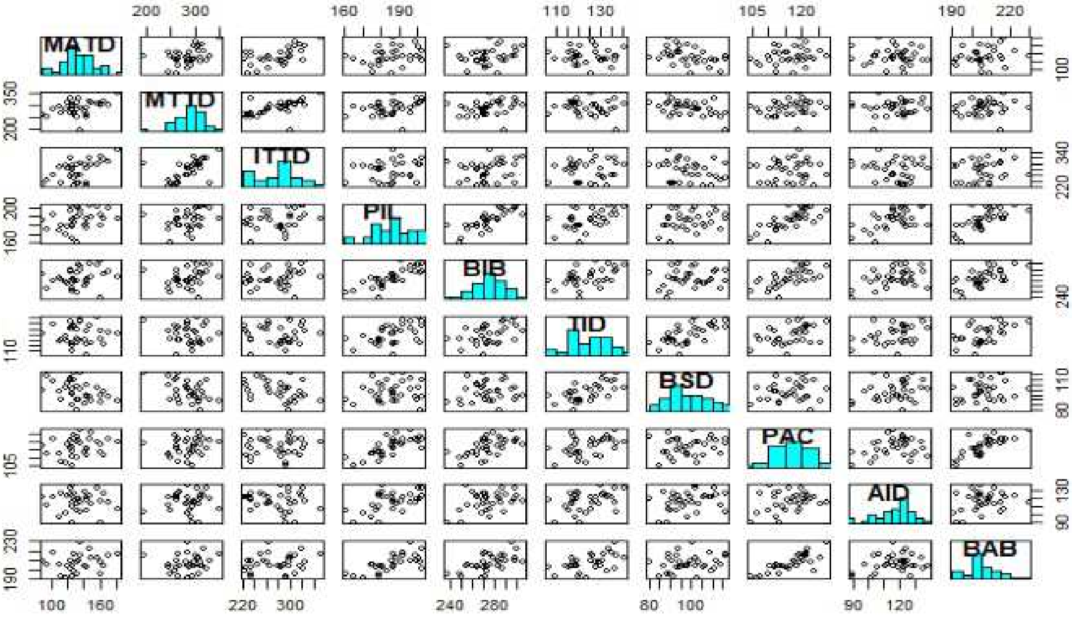

Figure 7: Scatterplots and histograms of measurements, female sample.

Correlation Matrices

As described in Chapter III, some measurements were eliminated due to redundancy or missing data. Pearson's product-moment correlation tests the relationship between two continuous variables and produces a correlation coefficient (r) that describes the strength of the relationship from –1 to +1, with relationships gaining strength as |1| is approached (Schober et al., 2018). In contrast, a Spearman correlation does not assume normal distribution and can be robust in the presence of outliers (Schober et al., 2018). A correlation matrix was made to compare relationships between thoracic measurements, while a separate correlation matrix was generated to compare relationships between pelvic measurements. Since some pelvic measurements appeared non-normally distributed, Pearson's product-moment correlations were used to assess relationships between thoracic variables, while Spearman's correlations were used to evaluate relationships between pelvic variables.

Table 6 describes the results of Pearson's correlation matrix generated for thoracic measurements. Thoracic measurements that were not first eliminated due to missing data were included in the correlation matrix, resulting in three total measurements. Two of these measurements were then eliminated due to statistical redundancy. ITTD was found to be strongly related to MTD (r > 0.7, after Schober et al., 2018), while MATD was found to be moderately related (r= 0.4-0.6) to both measurements. Since measurements appear to be well-related, all were eliminated apart from ITTD. Only ITTD was included in hypothesis testing as it appears to capture much of the same information as the other two thoracic variables and is most relevant to the research question this work addresses. Using this measurement alone allows the most information about the shape of the thorax to be captured via the simplest means.

Within the pelvic measurements, two were also eliminated due to statistical redundancy; results are summarized in Table 7. Eliminated pelvic measurements include only those that presented strong (r > 0.7 after (Schober et al., 2018) relationships with other pelvic measurements. Within the pelvic measurements, only Pubis-Ilium Length (PIL) and Acetabulo-

Symphyseal Length (PAC) were strongly related to other pelvic measurements. Because both showed strong relatedness to multiple pelvic measurements, they were eliminated prior to hypothesis testing. Since all other pelvic measurements collected capture either pelvic breadth (transverse plane) or depth (sagittal plane), it is unsurprising that PIL and PAC capture much of the same information, as both are diagonal measurements. The results of these correlation matrices serve to justify decisions to eliminate thoracic and pelvic variables by confirming that they are capturing information that is already accounted for by other measurements.

Table 6: Correlation matrix of thoracic variables for the whole sample, rounded to two decimal places. Excluded measurements are shown in gray boxes.

	1	2	3
1) Maximum Anteroposterior Thoracic Diameter	1.00	0.48	0.54
2) Maximum Transverse Thoracic Diameter	--	1.00	0.77
3) Inferior Transverse Thoracic Diameter	--	--	1.00

Table 7: Correlation matrix of pelvic variables for the whole sample, rounded to two decimal places. Excluded measurements are shown in gray boxes.

	1	2	3	4	5	6	7
1) Pubis-Ilium Length	1.00	0.64	0.42	0.00	0.32	0.68	0.75
2) Bi-Iliac breadth	--	1.00	0.52	0.10	0.21	0.69	0.56
3) Transverse Inlet Diameter	--	--	1.00	0.59	0.44	0.58	0.53
4) Bispinous Diameter	--	--	--	1.00	0.39	0.23	0.99
5) Anteroposterior Inlet Diameter	--	--	--	--	1.00	0.10	0.22
6) Bi-Acetabular Breadth	--	--	--	--	--	1.00	0.81
7) Acetabulo-symphyseal Length	--	--	--	--	--	--	1.00

Welch's t-test

Welch's t-tests were used to compare mean values for each of the six measurements included between males and females. The results are summarized in Table 8 and displayed in Figure 5. Welch's t-tests compare means between groups of normally distributed data and are preferable when sample sizes between groups are unequal, as is the case with the male and female groups in this work (Kim, 2019). All but one measurement yielded t-scores with 95% confidence intervals that do not contain zero, suggesting that most of these measurements are sexually dimorphic to some degree. These include Inferior Transverse Thoracic Diameter ($t = -4.067$), Anteroposterior Inlet Diameter ($t = 3.7984$), Transverse Inlet Diameter ($t = 3.855$) and Bi-Acetabular Breadth ($t = -2.1649$). The remaining measurement, Bi-Iliac Breadth, displayed the lowest t-score (-1.193) with 95% confidence intervals that included zero (-12.70, 3.18), suggesting minimal differences between male and female group means when compared to other measurements.

Overall, most means displayed significant differences between male and female groups. The largest difference in means between sexes belonged to Bispinous Diameter ($t = 6.999$), which is unsurprising as this dimension is known to be sexually dimorphic, as humans must maintain certain dimensions for successful childbirth (Walrath & Glantz, 1996). Both inferior thoracic and pelvic inlet measurements appear to be sexually dimorphic; inlet measurements are also expected to differ by sex as these dimensions influence the ease of childbirth in modern humans. Bi-Iliac Breadth showed the smallest difference in means when comparing male and female groups (t= Overall, these results indicate that most of the six measurements of interest are sexually dimorphic, justifying the decision to carry out hypothesis tests on the male and female samples separately.

Table 8: Summary of results of Welch's t-tests for included measurements, rounded to two decimals.

Measurement	Male Mean	Female Mean	t-score	95% CI
Inferior Transverse Thoracic Diameter	288.23	261.66	-4.07	-39.50, -13.64
Bi-Iliac Breadth	277.64	272.88	-1.2	-12.70, 3.18
Anteroposterior Inlet Diameter	111.68	119.86	3.80	3.76, 12.60
Transverse Inlet Diameter	122.14	129.51	3.86	3.54, 11.19
Bispinous Diameter	92.74	107.21	7.01	10.34, 18.59
Bi-Acetabular Breadth	209.73	204.62	-2.17	-9.81, -0.40

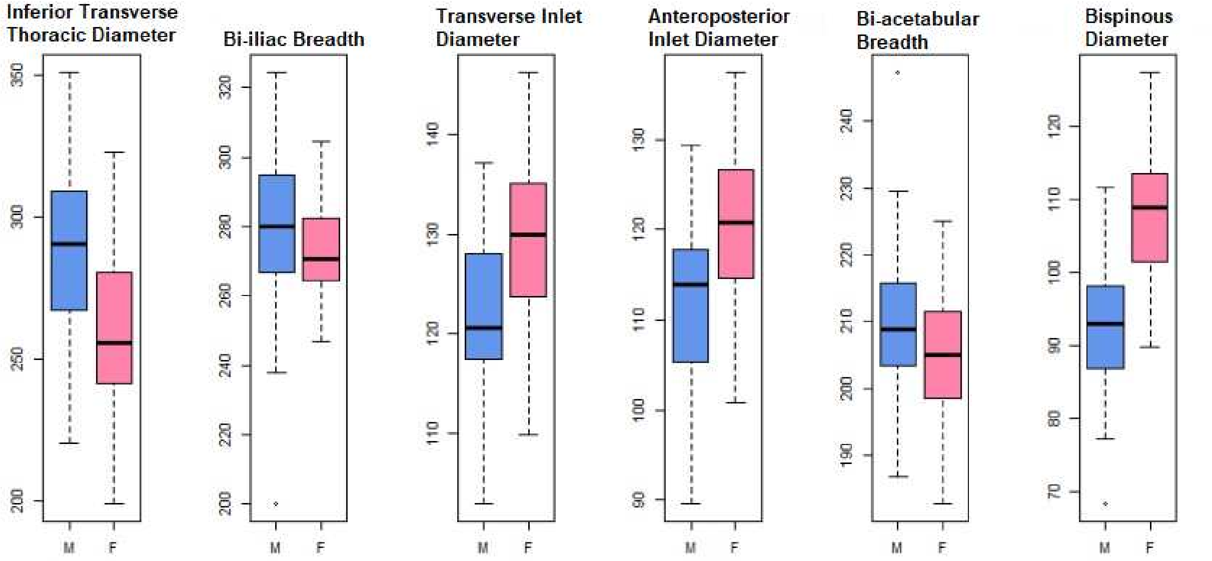

Figure 8: Boxplots showing means and ranges for each included measurement by sex.

HYPOTHESIS TESTING

Male Sample

In order to determine if the thoracic and pelvic measurements collected in this work are significantly related to each other, Pearson's product-moment correlation tests were carried out between Inferior Transverse Thoracic Diameter (ITTD) and each of the five pelvic measurements collected individually. The results of these tests are summarized in Table 9. Scatterplots were then generated to visualize these results and are shown in Figures 9-13. As previously noted, Pearson's product-moment correlation tests assess linear relationships between two continuous, normally distributed variables (Schober et al., 2018). Within the male sample, only two relationships between ITTD and pelvic measurements were found to be statistically significant, as their corresponding confidence intervals did not contain zero. These include ITTD and Transverse Inlet Diameter (r= 0.36, 95% CI [0.08, 0.57]), as well as ITTD and Bi-Acetabular breadth (r=0.31, 95% CI [0.03, 0.54]). All other measurements (Bi-Iliac Breadth, Anteroposterior Inlet Diameter, and Bispinous Diameter) did not display significant relatedness to ITTD. Although most relationships assessed here were not statistically significant, all relationships between thoracic and pelvic dimensions were generally weak (following conventional interpretation) within the male sample, with none surpassing r=0.35 (Schober et al., 2018). In this case, the null hypothesis that there are no significant relationships between ITTD and collected pelvic measurements cannot be rejected for BIB, APID, and BSD, as the 95% confidence interval for these relationships contains zero. For TID and BAB, the null hypothesis is rejected, offering support for the alternative hypothesis that there is a nonzero, significant relationship between TID and ITTD and BAB and ITTD, respectively, as the 95% confidence interval for these measurements does not contain zero. Generally, relatedness between dimensions of the pelvis and inferior thorax appears to be either nonexistent or weakly present in males, and confidence intervals are large for all relationships. Results indicate that Inferior Transverse Thoracic Diameter is not a significant predictor of pelvic breadth or depth in modern male *Homo sapiens.*

Table 9: Summary of results for Pearson's correlation tests performed on the male sample rounded to two decimal places; Inferior Transverse Thoracic Diameter abbreviated to ITTD.

Measurements Tested	Pearson's Correlation Coefficient	95% CI
ITTD and Bi-Iliac Breadth	0.23	-0.05, 0.48
ITTD and Transverse Inlet Diameter	0.36	0.08, 0.57
ITTD and Anteroposterior Inlet Diameter	0.00	-0.27, 0.28
ITTD and Bispinous Diameter	0.03	-0.25, 0.31
ITTD and Bi-Acetabular Breadth	0.31	0.03, 0.54

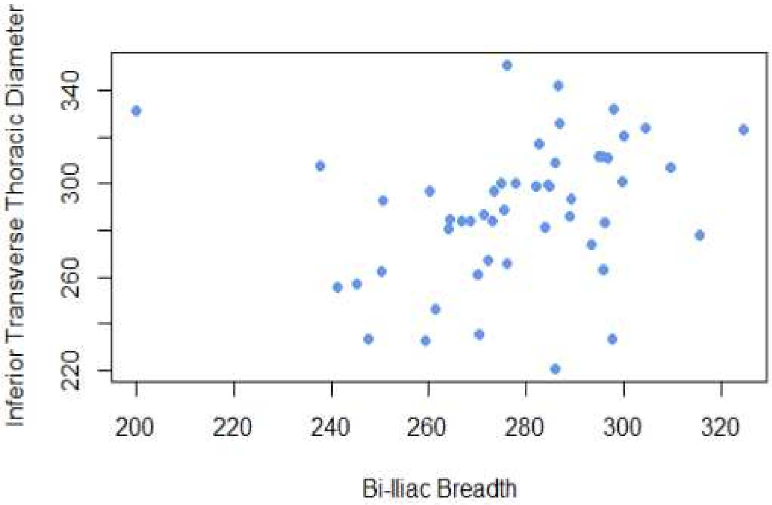

Figure 9: Scatterplot of ITTD and Bi-Iliac Breadth (Males)

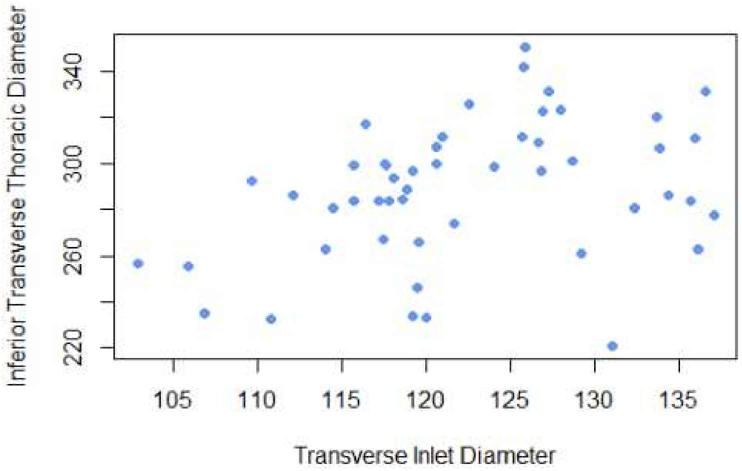

Figure 10: Scatterplot of ITTD and Transverse Inlet Diameter (males)

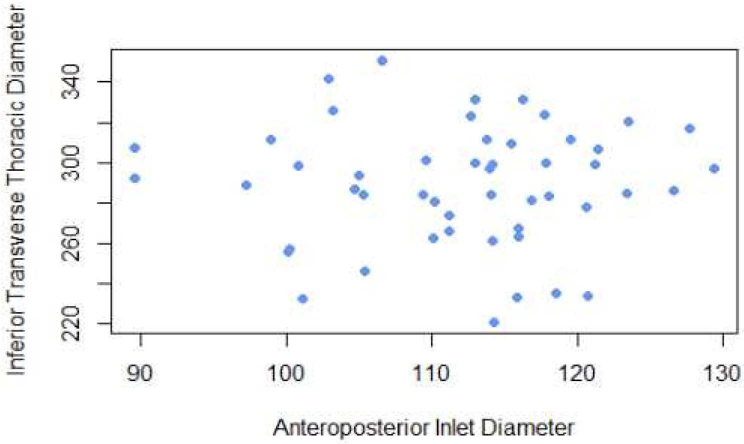

Figure 11: Scatterplot of ITTD and Anteroposterior Inlet Diameter (males)

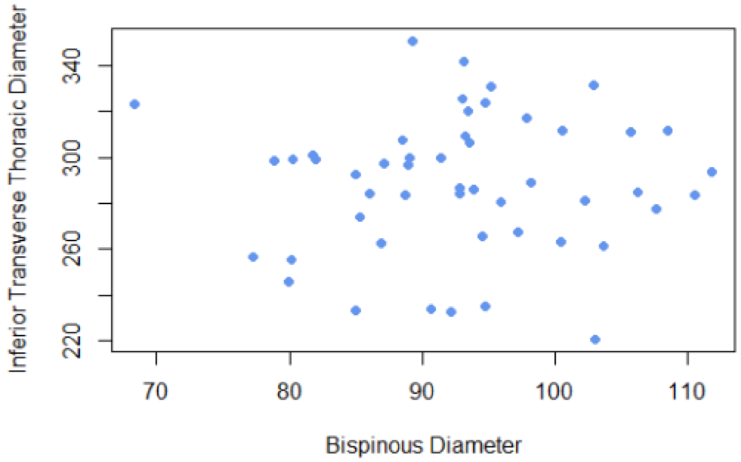

Figure 12: Scatterplot of ITTD and Bispinous Diameter (males)

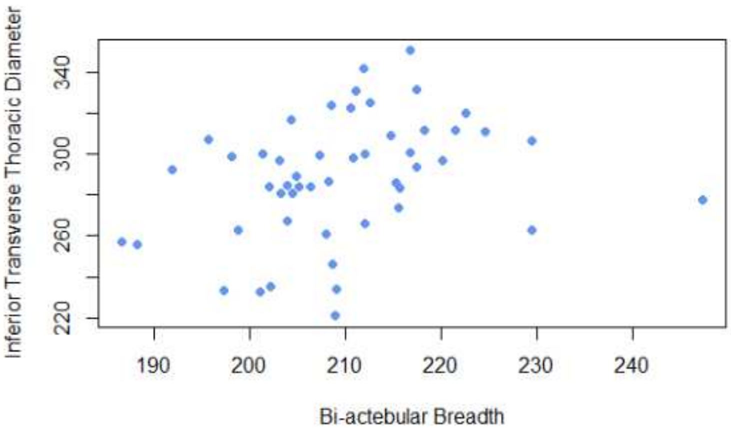

Figure 13: Scatterplot of ITTD and Bi-Acetabular Breadth (males)

Female Sample

To determine the relatedness between the thoracic and pelvic measurements collected in this work, Pearson's product-moment correlation tests were performed individually between Inferior Transverse Thoracic Diameter (ITTD) and the five pelvic measurements described in Chapter III. Scatterplots were generated to visualize the results of these tests and are displayed in Figures 14-18. The results of these tests are summarized in Table 10. Within the female sample, no significant relationships ($p<0.05$) were found between ITTD and the five pelvic measurements collected (Bi-Iliac Breadth, Transverse Inlet Diameter, Anteroposterior Inlet Diameter, Bispinous Diameter, and Bi-Acetabular Breadth), respectively. As with the male sample, all relationships between ITTD and pelvic measurements were relatively weak, with the highest Pearson's correlation coefficient belonging to ITTD and Bi-Iliac Breadth, $r=0.33$. As is the case with the male sample, confidence intervals are large for all correlation coefficients, and in the female sample, all 95% confidence intervals span negative and positive values. In this case, the null hypothesis that there is no significant relationship between thoracic and pelvic measurements cannot be rejected for any of the five pelvic measurements, suggesting that the alternative hypothesis of a nonzero, significant relationship between ITTD and collected pelvic measurements is not well-supported. In summary, these findings suggest there are no significant relationships between Inferior Transverse Thoracic Diameter and collected measures of pelvic breadth and depth in female modern *Homo sapiens.* As is the case with the male sample, these results indicate that inferior thoracic breadth is not a predictor of pelvic breadth or depth.

Table 10: Summary of results for Pearson's correlation tests performed on the female sample rounded to two decimal places; Inferior Transverse Thoracic Diameter abbreviated to ITTD.

Measurements Tested	Pearson's Correlation Coefficient	95% CI
ITTD and Bi-Iliac Breadth	0.32	-0.02, 0.60
ITTD and Transverse Inlet Diameter	0.18	-0.17, 0.50
ITTD and Anteroposterior Inlet Diameter	-0.10	-0.43, 0.25
ITTD and Bispinous Diameter	0.07	-0.28, 0.41
ITTD and Bi-Acetabular Breadth	0.08	-0.27, 0.41

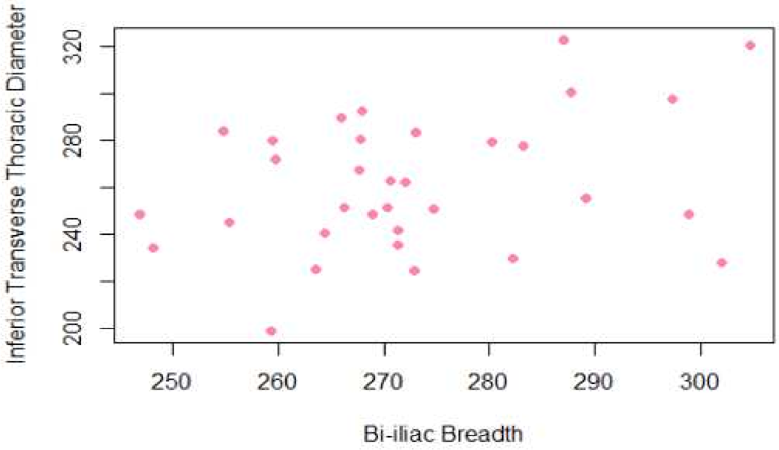

Figure 14: Scatterplot of ITTD and Bi-Iliac Breadth (females)

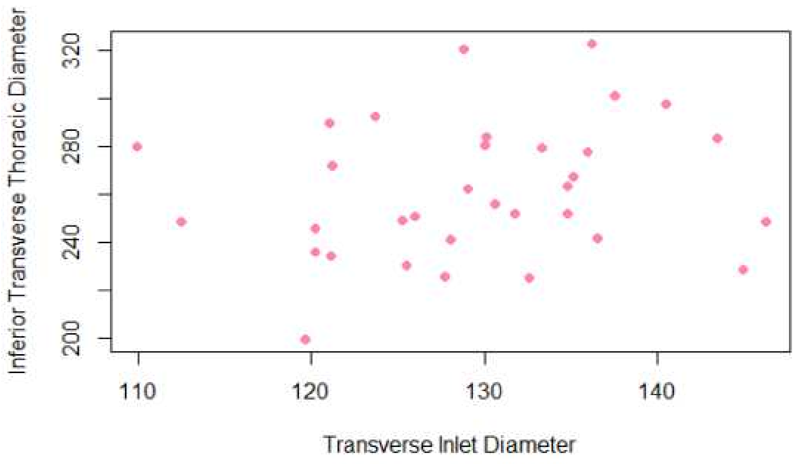

Figure 15: Scatterplot of ITTD and Transverse Inlet Diameter (females)

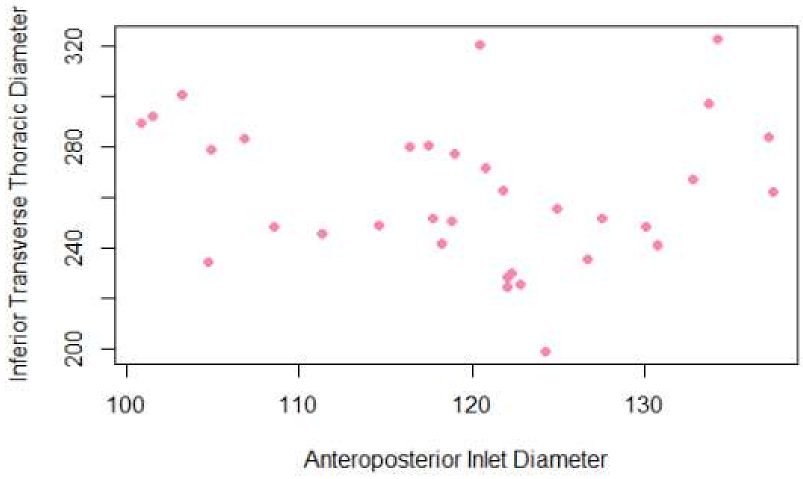

Figure 16: Scatterplot of ITTD and Anteroposterior Inlet Diameter (females)

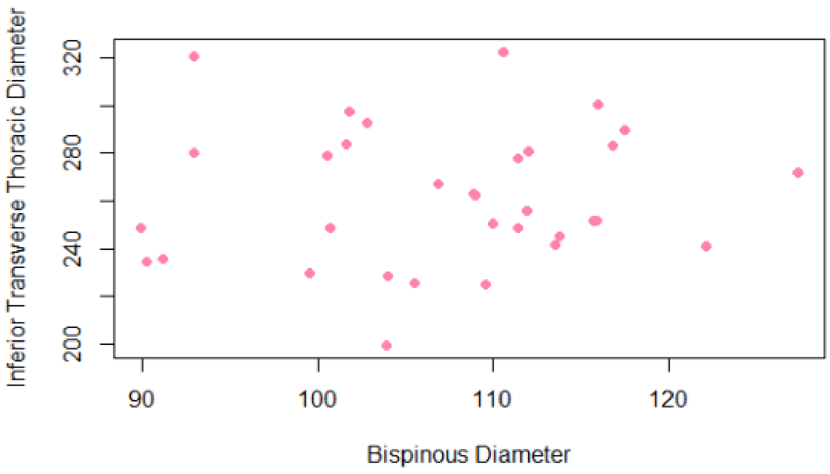

Figure 17: Scatterplot of ITTD and Bispinous Diameter (females)

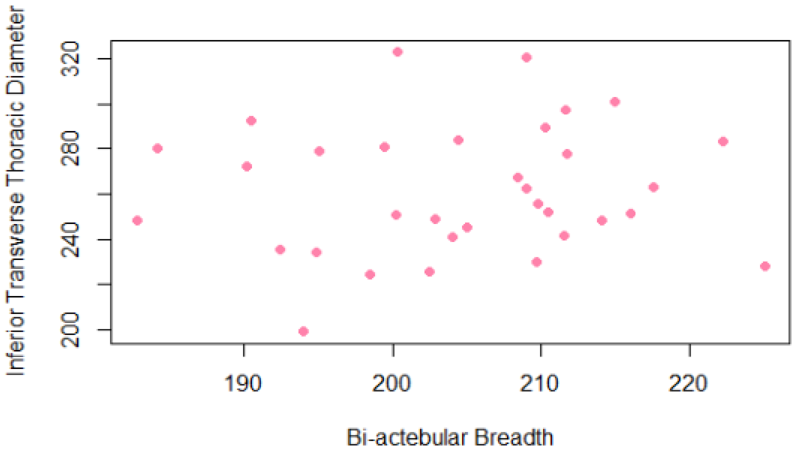

Figure 18: Scatterplot of ITTD and Bi-Acetabular Breadth (females)

CHAPTER SUMMARY

This chapter summarized the results of the statistical tests conducted on the sample to address the research question and hypotheses described in Chapter I. For the male sample, the null hypothesis that there is no statistically significant relationship between ITTD and pelvic measurements was upheld for three of the five pelvic measurements. The null hypothesis was only able to be overturned for the relationships between ITTD and Transverse Inlet Diameter, as well as ITTD and Bi-Acetabular Breadth within the male sample. These results indicate statistically significant but relatively weak relationships between these dimensions. Within the female sample, the null hypothesis was upheld for ITTD and all collected pelvic measurements. Overall, results indicate that for both male and female modern *Homo sapiens*, inferior thoracic width is a poor predictor of pelvic breadth and depth.

CHAPTER V

DISCUSSION AND CONCLUSION

The aim of the present study was to identify and understand morphological relationships between the thorax and pelvis in modern humans in the context of the torso integration hypothesis and its application to the interpretation of hominin body shape. This information is increasingly relevant as new and old fossil finds cause researchers to question previously established narratives of changes to hominin body shape in the fossil record. In turn, the methods used to establish these narratives necessitate examination. In summary, this study sought to answer the question of whether the torso integration hypothesis, as proposed in early hominins and *H. erectus*, applies to modern *Homo sapiens* (Torres-Tamayo et al., 2018, 2020). To address this question, relationships between linear measurements of the thorax and pelvis were assessed via statistical tests described in Chapter III.

RELATIONSHIPS WITHIN THE TRUNK

It has long been hypothesized that the inferior thorax tracks in breadth and shape with the superior pelvis of anthropoid primates, Australopiths, and *H. erectus* (Bastir et al., 2020; Torres-Tamayo et al., 2018; Jellema et al., 1993). However, few studies exist that evaluate this relationship in modern *Homo sapiens* (Torres-Tamayo et al., 2018). The results of the current work, reported in Chapter IV, appear to imply that this relationship is either not present or extremely weak in modern humans. Although some statistically significant relationships between thoracic breadth and pelvic dimensions were found within the male sample, the relation between these areas is weak across the entire sample and nearly nonexistent in the female sample (see Tables 7 and 8). Generally, the expected correspondence between the inferior ribcage and superior pelvis originally described by (Schultz, 1961) does not appear to exist in modern *Homo sapiens* based on the current sample. Relationships between inferior thoracic breadth and Bi-Iliac Breadth are not consistently stronger when compared to other dimensions of the pelvis, and all relationships between thoracic and pelvic dimensions are weak. While this may be unsurprising due to the functional differences of these areas, several factors potentially contribute to these results and warrant further discussion.

Sexual Dimorphism in the Human Pelvis

Previous research suggests that relationships between thoracic and pelvic breadth differ between sexes in modern *Homo sapiens* and that correspondence between these areas exists only in the absence of sexual dimorphism (Torres-Tamayo et al., 2018, 2020). As noted in Chapter IV, the measurements analyzed are sexually dimorphic (differences in means between males and females are depicted in Figure 5 in Chapter IV). Previous research has indicated that modern male *Homo sapiens* tend to show wider thoraces relative to pelves, while females appear to have wider pelves and smaller thoraces, though this relationship may depend on population (Torres-Tamayo et al., 2018). The results of Welch's t-test performed on this sample indicate sex-driven differences in thoracic breadth, while Bi-Iliac Breadth is, interestingly, similar between sexes. Generally, relationships between these areas differ by sex based on the current sample; regardless of statistical significance and strength of relationships, there appears to be very little common patterning between sexes. Of the weak and/or statistically insignificant relationships observed through Pearson's product-moment correlations, there appear to be relatively stronger relationships between inferior thoracic breadth and superior pelvic breadth (when compared to other pelvic dimensions) in females. However, only in males are any of these relationships significant enough not to be explained by chance alone, and most relationships observed have large 95% confidence intervals that span negative and positive values, indicating that it is possible that no relationships exist between measured thoracic and pelvic dimensions. There is little consistency between the sexes beyond these observations.

Given the sex-driven patterns found in modern human torsos by this and previous works, it is important to understand what contributes to sexual dimorphism in the trunk for both early and modern hominins (Torres-Tamayo et al., 2018, 2020). As discussed in Chapter II, modern *Homo sapiens* face unique obstetric challenges as a result of needing to birth encephalized infants. The comparatively small brain sizes seen in Australopiths, as well as their wide but anteroposteriorly shallow pelves, are thought to suggest different birthing mechanisms than those seen in modern humans (DeSilva et al., 2017; Gruss & Schmitt, 2015). Generally, it has been proposed that these hominins experienced a non-rotational or semi-rotational birth (DeSilva et al., 2017; Gruss & Schmitt, 2015). In contrast, modern female humans must maintain pelvic proportions that allow an encephalized infant's head and shoulders to pass through. In contrast to the wide, platypelloid pelves associated with *Australopithecus*, anteroposterior expansion (as seen in modern humans and *H. erectus*) is thought to be necessary for successful birthing of encephalized neonates (Gruss & Schmitt, 2015). Previous exploration of the relationships between the thorax and pelvis in modern humans suggests that the covariance of dimension and curvature of these areas may differ by both sex and population (Torres-Tamayo et al., 2018, 2020). Given these differences, it is relevant to consider whether sexual dimorphism in the pelvis and/or thorax should influence the expectation of torso integration in hominin groups like *H. erectus*.

Within the fossil record, pelvic remains with preserved ilia that have been assigned to *H. erectus* appear much wider than KNM WT-15000. These remains are identified as female, apart from one individual, and are listed in Table 1 in Chapter II. An in-depth discussion on the extent to which *H. erectus* can be considered sexually dimorphic is outside the scope of the current work. However, it appears to be the case that *H. erectus* pelvis was incredibly sexually dimorphic and displayed anteroposterior expansion that is likely related to parturition when compared to earlier hominins, though it should be noted that inclusion of the very broad Gona pelvis in *H. erectus* can indicate "either very high levels of sexual dimorphism or great intraspecific variation in body size" (Churchill & Vansickle, 2017; Gruss & Schmitt, 2015 p. 8;). Regardless, the torso integration hypothesis itself only postulates a relation between the inferior thorax and superior pelvis (ilia), meaning that sexual dimorphism in the pelvis below the ilia (i.e., critical birth dimensions) should contribute minimally to the strength of this proposed relationship. Sex-related differences in Bi-Iliac Breadth, rather than critical birth dimensions, should be considered when assessing the extent to which pelvic sexual dimorphism may contribute to the applicability of the torso integration hypothesis to hominin groups.

The present study suggests only small differences in superior pelvic breadth (bi-Iliac breadth) between sexes in modern *Homo sapiens* (see Figure 5, Table 6 in Chapter IV). Rather, significant differences between sexes are mainly seen in pelvic dimensions that are critical to successful childbirth, as is expected. Bi-Iliac Breadth in modern *Homo sapiens* appears to be similar between sexes, with the difference between average BIB being only five millimeters. In comparison, the average measure of Bispinous Diameter, a critical birth dimension, in males and females differs by 15 millimeters. Since Bi-illiac breadths are similar between sexes, if the torso integration hypothesis holds true for modern humans, one should expect to see similar overlap in dimensions of inferior thoracic breadths in males and females. However, this does not appear to be the case. In terms of the portions of the trunk that are described by the torso integration hypothesis, it is only in the breadth of the inferior thorax where modern *Homo sapiens* appear to differ significantly from one another by sex.

Sexual Dimorphism in the Thorax

As previously noted, reconstructions of hominin thoraces are difficult to undertake, and the many elements of the thorax are rarely well-preserved. As detailed in Chapter II, initial descriptions of the ribcage of KNM WT-15000 suggest a rather narrow and shallow, modern-human-like ribcage (Jellema et al., 1993). However, a recent reconstruction that accounts for additional vertebral and rib remains has suggested that KNM WT-15000 instead possessed a wide, deep thorax, more similar to that of Kebara 2 (Bastir et al., 2020). While the rarity of well-preserved thoracic material in the fossil record makes discussing sexual dimorphism in the thorax of *H. erectus* difficult, sexual dimorphism in the thorax of modern humans is well documented. The explanation of this pattern in modern humans may, in turn, help to form hypotheses about sexual dimorphism in the thoraces of past hominin groups.

Research on modern humans has documented many sex-related differences in the thorax of modern humans (Garcia-Martinez et al., 2016; LoMauro Aliverti, 2018). As is observed in this work, research suggests males generally tend to display ribcages that are wider than those of females, specifically in the inferior portion; in addition, male ribcages appear to be shorter with lower-placed sternums than females (Garcia-Martinez et al., 2016). If the torso integration hypothesis, as proposed in non-human primates and hominins, were to also apply to modern humans, it should be expected that males display, on average, significantly larger Bi-Iliac Breadths than females. However, as suggested by the current work and previous research, this is not the case (Torres-Tamayo et al., 2018).

Further evidence exists to suggest that these observable differences in thorax size and shape between sexes may somewhat be related to differences in the breathing patterns of modern humans. Specifically, it has been proposed that the relative difference in lean mass between modern males and females necessitates greater oxygen intake for the former, which in turn may demand a greater functional thoracic size achieved partially by mediolateral expansion of the ribcage (Garcia-Martinez et al., 2016). It is the case that studies of healthy adults have found that while breathing movements were uniform between sexes at different ages, deep breathing movements did tend to differ between males and females (Ragnarsdóttir & Kristinsdóttir, 2006). Modern human research has additionally indicated that male thoraces tend to be especially broader in the inferior portion when compared to females (Garcia-Martinez et al., 2016). Generally, then, modern human data indicates that sex-based differences in the inferior thorax and the thorax as a whole are most readily explained by differences in breathing patterns and relative oxygen intake. The wider, deeper thorax of modern human males has been proposed to be advantageous for intense physical activity; this has also been suggested to be true of the wider, deeper thoraces of neandertals when compared to modern humans (Bastir et al., 2022; Garcia-Martinez et al., 2016). Understanding the degree and source of sexual dimorphism in the ilia and thoraces of hominin groups may then be significant for evaluating the extent to which torso integration should be expected.

Considering Hominin Body Shapes

While the available thoracic material that can be reliably assigned to *H. erectus* and *H. neanderthalensis* does not necessarily allow reliable assessment of sexual dimorphism of the thorax in these hominin groups, the results from this and previous studies indicate that the thorax and pelvis vary independently of each other in modern humans, and potentially even in extant anthropoids (Torres-Tamayo et al., 2018, 2020; Ward et al., 2015). Not only does it appear that there is no integration *between* these structures, but studies of modern humans have also indicated a lack of integration (presence of modularity) *within* both the thorax and the pelvis. Specifically, portions of the ribcage appear to vary in size independently of one another in modern humans; generally, it appears that the modern human upper thorax is less variable than the lower thorax, and both follow different growth patterns throughout life (Bastir et al., 2013). Similarly, the pelvis also appears to be modular, not only in modern humans but in nonhuman primates. Both genetic and morphological evidence indicate that the ilium varies separately from the ischium and pubis, which appear integrated with each other (Lewton, 2011).

As noted in Chapter II, differences in neandertal and modern human body shape often reference the trunk as a unit and are explained mainly in the context of climate, though differences in behavior, locomotion, and energy requirements have also been used to explain these changes (Ocobock et al., 2021; Stewart et al., 2019). In modern humans, population-level differences in the portions of the trunk relevant to the torso integration hypothesis have been linked to climatic adaptation. Specifically, modern populations that inhabit higher latitudes appear to have longer ribs than those that live closer to the equator; this relationship is seen in the inferior ribs (7-11) rather than the entire thorax (Garcia-Martinez et al., 2018). It is well accepted that upper pelvic breadth (Bi-Iliac Breadth) follows a similar pattern, with studies of modern human populations showing an inverse relationship between Bi-Iliac Breadth and climatic temperature (Ruff, 1991). It also appears that this pelvic patterning holds true for premodern members of the genus *Homo.* Generally, higher-latitude hominins appear to have larger Bi-Iliac Breadths than low-latitude ones despite generally displaying wider body breadths than modern humans (Ruff, 2010). Specifically, the difference between OH 28 and the "nearly contemporaneous" Atapuerca 1 individual's Bi-Iliac Breadth appears to mirror the "average 3cm difference between modern tropical and higher latitude populations" (Ruff, 2010, p. 176). However, whether ecogeographic patterning of trunk breadth observed in modern humans is present to the same extent in the thoraces of past hominin groups remains difficult to assess. These comparisons of premodern hominin Bi-Iliac Breadths across latitudes are limited to ten individuals that comprise at least four different species, while preserved thoraces are even more scarce in the human fossil record. Regardless, it does appear that in modern humans, climate influences breadth in the pelvis and thorax similarly despite the two appearing to vary rather independently of each other.

If it is accepted, as many have suggested, that the plesiomorphic condition in the genus *Homo* is one of a wide thorax and pelvis when compared to modern humans, it is modern human morphology that demands explanation. Considering that climate appears to influence the upper and lower portions of the trunk similarly in modern humans (i.e., in corresponding to an increased/decreased breadth), it is relevant to consider the trunk as a unit when assessing climate-driven modern human variation. However, despite the homogeneity of the sample used in the current work (70% of the individuals reported their race as white, indicating that most were likely of European descent), marked differences in inferior thoracic breadth were still found between sexes. Of those that reported race, within the female sample, only 24% identified as something other than white, while 22% of males reported the same, indicating that European descent was likely similarly proportioned between both samples; however, it is not clear if populations associated with different climates are equally represented here due. Regardless, climatic adaptations in this appear to be a poor explanation of the difference in thoracic breadth observed between sexes when considering the similarity of Bi-Iliac Breadth within the current sample (see Figure 5 in Chapter IV).

Overall, the results presented in Chapter IV indicate little relation between pelvic and inferior thoracic breadth in modern *Homo sapiens* individuals. While modern human variation in these areas has been described in the context of climatic differences, this does not readily explain the results obtained in the current work. Instead, it appears that the relation between these areas differs by sex, which is somewhat corroborated by research indicating sexual dimorphism in the inferior ribcage that is potentially related to breathing differences (Garcia-Martinez et al., 2016; Ragnarsdóttir & Kristinsdóttir, 2006). Whether or not a wide thorax and pelvis are plesiomorphic within the genus *Homo*, results indicate that when understanding modern human variation and/or deviation from ancestral conditions, the upper and lower portions of the trunk may be best considered separately.

CONCLUSION

The purpose of this study was to address the research question of whether the torso integration hypothesis applies to modern *Homo sapiens*. In order to achieve this, relationships between collected measurements of the thorax and pelvis of 84 living individuals were collected using CT data and were subsequently assessed using Pearson's correlation tests. Utilization of CT data allowed measurements to be collected on articulated structures, preventing inaccuracy due to reconstruction error. However, this work faces several limitations. The sample utilized here is mainly made up of white males. Additionally, many individuals included in the sample are aged 60-79. Ideally, a sample would include many individuals from different populations, equal in number across age ranges and sexes, so that population, age, and sex-related differences can be assessed at once. Results have indicated that, based on the current sample, relationships between dimensions of the thorax and pelvis are generally weak or non-existent, making it unlikely that the torso integration hypothesis is applicable to modern *Homo sapiens*.

As previously stated, it is generally accepted that modern human body proportions are first seen in *H. erectus,* with KNM-WT 15000 providing evidence of a shift toward narrow thoraces and pelves coupled with long limbs (Holliday, 2012; Walker & Leakey, 1993). neandertal anatomy, in comparison, is often viewed as a deviation from this pattern, evidenced in their wide thoraces and pelves, coupled with short limbs (Ocobock et al., 2021). Many researchers now agree that *H. erectus* likely displayed a stocky, wide body, more like neandertal than modern human morphology. New reconstructions of the thorax of KNM-WT 15000 coupled with preserved *H. erectus* pelvic remains all suggest greater width in the trunk of *H. erectus* than initially thought (Bastir et al., 2020). The torso integration hypothesis, while initially proposed in nonhuman primates, was later hypothesized in *Australopithecus* (Schmid, 1983; Schmid et al., 2013; Schultz, 1961). This idea was subsequently referred to when reconstructing the nearly complete KNM-WT 15000, with the expectation being that the ribcage and ilium should correspond to each other in breadth (Jellema et al., 1993). However, little evidence exists to suggest that this pattern should be expected in later members of the genus *Homo*; studies of nonhuman apes and modern humans (including this one) suggest that this pattern is either not present or more complex than initially thought.

Whether wider-than-expected pelves imply wide thoraces in premodern hominins (as they do not appear to do so in modern humans) is difficult to assess due to the incomplete nature of the fossil record. Morphological patterns observed in extant primates (human and nonhuman) do not always necessarily correspond to those seen in the past. However, observations from extant populations can shape expectations and guide the questions asked when interpreting and reconstructing hominin fossils, as they have historically. If the same patterns of trunk integration exist in modern *Homo sapiens* and our recent ancestors, trends in hominin trunk shapes may be better explained by selective pressures acting on the inferior thorax or upper pelvis separately. Conversely, if the pattern observed in modern *Homo sapiens* is not shared with other members of the genus *Homo*, then there is reason to seek an explanation for our recent deviation from this pattern.

While the increasing accessibility and availability of CT data for studies of modern humans allow articulated structures to be measured with accuracy, the fossil record is fragmented, and our understanding of it is thoroughly dependent on preservation, access, and discovery. Perhaps more importantly, the expectations and biases held by researchers often influence shared understandings of our own human prehistory. If it is the case that thoracic and pelvic breadth covary in *H. erectus,* unlike what has been observed in modern humans, new reconstruction of the thorax of KNM-WT 15000 would suggest a much wider Bi-Iliac Breadth for this individual than initially thought (Bastir et al., 2020). Other pelvic remains assigned to *H. erectus* are, in fact, much broader than KNM-WT 15000's reconstructed pelvis and do suggest a wide pelvis (in comparison to modern humans) was the norm for all members of genus *Homo* that modern humans depart from (see Table 1).

Whether or not *H. erectus* diverges from or follows the observed lack of relation within the modern trunk is partially what stands to determine whether these pelvic remains imply an ancestral broad thorax. If it is instead the case that *H. erectus* lacked a strong, predictable relation between the dimensions of the inferior thorax and superior pelvis, then the narrowly reconstructed pelvis of KNM-WT 15000 does not necessarily demand a correspondingly narrow, modern-human-like thorax. If so, this would not contradict the newer, broader reconstruction of this individual's thorax and instead may still imply a broad, neandertal-like thorax was ancestral within the genus *Homo* even if the pelvis of KNM-WT 15000 accurately represents *H. erectus* pelvic morphology (Bastir et al., 2020).

As previously noted, the most well-preserved thoraces that have been assigned to *H. erectus* and *H. neanderthalensis* (belonging to KNM-WT 15000 and Kebara 2, respectively) are both believed to belong to male individuals. Due to their completeness, both individuals bear a great amount of influence in interpretations of thoracic morphology for their respective species, and recent reconstruction of KNM-WT 15000 has implied many thoracic affinities between these individuals (Bastir et al., 2020). Although many of the individuals that contribute to our understanding of neandertal thoraces are male, even the female Tabun I inferior thorax appears to fall outside the range of modern human variation in width, suggesting that in both sexes, neandertal thoraces tend to differ from those of modern humans (Weinstein, 2008). Generally, two things remain true: in modern humans, male ribcages tend to be wider and deeper inferiorly compared to females, while similar observations have been made when comparing modern human thoraces to neandertal and now *H. erectus* thoraces.

While it is not the goal of the current work to determine the degree to which torso integration or thoracic sexual dimorphism was present in later hominins, the weight that understanding thoracic and pelvic integration bears on interpreting the human evolutionary past is important to consider. Whether the wide pelves attributed to *H. erectus* imply equally wide thoraces influences the understanding of when shifts in hominin trunk shape took place. In turn, whether the wide thoraces and pelves observed in neandertals represent an ancestral or derived condition changes the lens through which their, and our own, morphology is interpreted.

Observing patterns in modern humans is the first of many steps to determine their causes, which in turn supplement understanding of patterns observed in the past.

While studies on the potential relationships between inferior thoracic and pelvic variation in modern humans are few, this work has suggested that there is little relation between breadth in these anatomical areas, which is consistent with previous research (Torres-Tamayo et al., 2018). As stated earlier, previous work also suggests that there may be population-level differences in this observed pattern. Some populations have been found to display a greater degree of sexual dimorphism in the pelvis, while in other populations, sexual dimorphism is more readily observed in differences in thoracic breadths, as is seen in this work (Torres-Tamayo et al., 2018). As previously noted, many have linked climatic conditions to size differences in both anatomical areas (Garcia-Martinez et al., 2018; Ruff, 1991; Weinstein, 2017). Considering this, future research can benefit from studying pelvic and thoracic relationships on large samples that make use of data from populations that have historically inhabited a variety of climates. This should allow a better understanding of how the pelvis and thorax as individual units are influenced by climate while helping to establish whether inferior thoracic dimensions should imply similar pelvic dimensions in modern humans and, potentially, hominins.

As discussed in Chapter II, many researchers have suggested different advantages and disadvantages of both wide and narrow pelvic and thoracic breadths when interpreting modern human, neandertal, and *H. erectus* morphology. Most of these advantages have been described in the context of locomotion, thermoregulation, and birth (see Table 2). However, few studies of modern humans with differing body shapes exist that provide tests of these proposed advantages. Future research on hominin body shape can benefit from seeking to test hypothesized relationships between pelvic or thoracic breadth and proposed advantages (i.e., efficiency for diverse types of locomotion) in modern humans. Additionally, medical literature can be drawn upon to support an understanding of these potential relative advantages. As previously noted, some research has shown relationships between pelvic proportions and knee injury rates (Emami et al., 2007; Messier et al., 1991). Future research can then benefit from using modern human data to better understand and evaluate the proposed advantages of differences in trunk shape observed in hominin groups.

In conclusion, the present study suggests that inferior thoracic breadths correspond weakly, if at all, to superior pelvic breadths in modern *Homo sapiens*. This is contrary to the common expectation that thoracic and pelvic widths correspond to each other in hominin groups like Australopiths and *H. erectus.* Thoracic breadths appear to differ by sex to a greater degree than pelvic breadths in modern *Homo sapiens,* though this may be dependent on population history (Torres-Tamayo et al., 2018). Further research that incorporates diverse populations is needed to establish a reliable pattern of torso integration (or lack thereof) in modern *Homo sapiens*; this should serve to broaden understanding of trends in hominin body proportions.

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